

THE SOLDIERLESS TERMITES OF AFRICA
(ISOPTERA: TERMITIDAE)



BY
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Centre for Overseas Pest Research

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By W. A. SANDS

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SYNOPSIS

The soldierless termites from the African continent, hitherto all included in the genus *Anoplotermes*, are fully revised. They are shown to belong to the subfamily Apicotermittinae, which is expanded to include all related forms. The subfamily Amitermittinae, in which they were previously classified, becomes a junior synonym of Termitinae. Sixty species (51 new) and 16 genera (all new) are recognized. Seven specific names are found to be synonymous and two species previously assigned to *Anoplotermes* are transferred to genera in other groups of termites. Keys are given to genera and species, and the phylogeny of the whole family Termitidae is discussed. The classification adopted is based largely on the results of multivariate analyses of coded characters and measurements, but is modified to conform to conventional standards where necessary.

INTRODUCTION

THIS work was begun as a revision of the African species of the genus *Anoplotermes*. These soldierless termites have long been known throughout the tropical parts of the continent as common inhabitants of the soil and the mounds of other groups of termites. Ecological observations by Kemp (1955), Harris (1963) and Sands (1965a) have shown that they are among the most important constituents of the soil fauna, being second only in abundance to *Microtermes* (Macrotermitinae). They are not distinguished by any striking external feature other than the absence of a soldier caste, and have often been confused with other Termitidae, sometimes widely unrelated. In the course of the study it soon became clear that more than one genus was involved. With few exceptions they feed on soil and superficially look very like various Termitinae and Nasutitermitinae with the same habit. One slight difference from the majority of these is visible only in the live insects, that is the curious transversely striped appearance of the abdomen as the worker moves about. It arises from the folding of the thin translucent cuticle over the powerful transverse and longitudinal muscles that produce the phenomenon referred to in subsequent sections as abdominal dehiscence. This is not universal in the soldierless termites, but in Africa there are few exceptions. When molested by predators such as ants, or when grasped by forceps and placed in alcohol, the abdominal muscles contract convulsively and the abdomen ruptures across a line of weakness behind the first tergite. The intestines erupt through the gap and themselves tend to burst, scattering their slimy contents. This reaction is elicited even when the termite is only held to the substrate by the extreme tip of an appendage such as the tarsus; no contact with or pressure on the abdomen is required to set off the mechanism. Fragility of the body wall and intestines as a defensive mechanism against Doryline ants in *Cubitermes* was noted by Williams (1959). There is no doubt that the contents of the worker hind gut of many soil-feeding termites are offensive to ants. *Speculitermes* in India have been observed by the present author to whip the tip of the elongated mobile abdomen forwards to deposit a blob of rectal contents on the head of a predator. The same response was elicited to the collector's forceps. No such behaviour has yet been recorded from Africa but the alternative suicidal defence of abdominal dehiscence has developed to a high degree. In some genera the sclerotized spiny armature of the enteric valve appears to form a linking structure between the two sections of the hind gut. This probably prevents the rupture at the valve from taking place too easily, as it is apt to do in less specialized forms. In *Ateuchotermes* the link snaps across the narrower part of its sclerotized stem when pulled hard enough. In some *Anenteotermes* the dual link has a click-over action, again giving way suddenly to excess tension. These parallel though distinct mechanisms may result in a build-up of hydrostatic pressure and a correspondingly more devastating defensive explosion when the release occurs. A similar suicidal type of defence has been observed in Neotropical species of *Anoplotermes* (A. Mathews, personal communication). The rarity of the soldier caste in *Speculitermes* and its absence in other genera attests the effectiveness of these methods of deterring predators.

Their very lack of a soldier caste has led to this group of termites being regarded

as an intractable taxonomic problem, avoided by most systematists. This accounts for the small number of species described and the paucity of material in collections. Eleven species were previously included in the genus from Africa. The holotype, syntypes and paratypes of all these have been examined and lectotypes selected and designated where necessary. Of the named species of *Anoplotermes*, *A. lateralis* (Walker) is in fact a *Microcerotermes*, and *A. pallidipes* (Sjöstedt) is a *Pericapritermes*. *A. placidus* Silvestri, *A. sanctus* Silvestri and *A. sedatus* Silvestri all become junior synonyms.

The nomenclatural adjustments resulting from the removal of two species to other genera are set out formally below.

***Microcerotermes lateralis* (Walker) comb. n.**

Termes lateralis Walker, 1853 : 523. Holotype imago, sex indeterminable, SIERRA LEONE, in BMNH.

Anoplotermes lateralis (Walker); Silvestri, 1914 : 65.

***Pericapritermes pallidipes* (Sjöstedt) comb. n.**

Eutermes pallidipes Sjöstedt, 1900 : 172. Syntype imagos, CAMEROON: Kribi, in Zoologisches Museum, Berlin.

Anoplotermes pallidipes (Sjöstedt); Sjöstedt, 1926 : 289.

To the remaining six of the original species have been added three species-names initially placed in genera of Termitinae, and now found to belong to this group. The type-species of these too have been examined and lectotypes designated. These changes are not unusual and no more than were anticipated. The unexpected feature of this work has been the discovery of a complex of 60 species for which both imago and worker castes are available. None of these or the earlier species can be attributed to *Anoplotermes*, which is a genus confined to the Neotropical region (an Indian species described by Roonwal and Chhotani (1960) is unlikely to be congeneric with the type-species, *A. pacificus* Muller).

The African species are now divided into 16 genera of which eight are monotypic, two have two species, and the remainder have three, four, six, eight, 10 and 17 species respectively. This pattern of subdivision is similar to that found in the subfamily Nasutitermitinae for the same region by Sands (1965). Many of the species described here have to be based on single nest-series owing to shortage of specimens. Only in the commonest species is there abundant material to establish the range of variation. Where closely related forms collected from widely separated localities differ in some characters, they are treated as distinct species until intermediates are found. Some species now recognized may consequently be future synonyms. On the other hand the alates are feeble fliers with poor dispersive powers and local speciation seems to have been frequent. A number of distinct species are known from the worker caste alone. These are not named because in a group as difficult as this it is advisable to have all castes before descriptions are formally made. The existence of more species shows that the work is not complete for Africa, whilst for other zoogeographical regions the group has scarcely been touched.

The importance of the soldierless termites as soil-working organisms in the Tropics is evident. The new information on their morphology raises the question of the adequacy of the existing subfamilial classification. The confusion this arouses is illustrated by the discussion of their relationships by Roonwal and Chhotani (1966). This confusion can be resolved by certain alterations which are discussed in detail in the section on phylogeny. The soldierless forms and their relations are removed from the Amitermitinae and placed in the Apicotermitinae. The subfamily allocation is therefore omitted from the title to this paper.

In order to emphasize the uniformity of the soldierless termites, and their relationship to *Anoplotermes*, the first-named member of the group, all the generic names used here begin with the same letter. This was achieved by the choice of names expressing their unarmed, passive condition.

MATERIAL

A total of 598 nest-series are listed in this revision. These represent about 95% of the material examined, the remainder being of single castes that do not match any of the recognized species.

Much of the material has been collected by members of the Termite Research Unit (Ministry of Overseas Development) and is deposited at the British Museum (Natural History). Types and other specimens have been obtained on loan, through the courtesy of specialists and others mentioned in the acknowledgements from the following museum collections:

Naturhistoriska Riksmuseum, Stockholm; Silvestri collection, Istituto di Entomologia Agraria 'Filippo Silvestri', Portici, Naples (Silvestri Coll., Ist. Ent. Agr.); American Museum of Natural History, New York (AMNH); National Collection of Isoptera, Plant Protection Research Institute, Pretoria (N.C.I., Pretoria); Musée Royal de l'Afrique Centrale, Tervuren; Swiss Tropical Institute, Basle; University of Lovanium, Kinshasa.

The abbreviations given in parentheses are those used in the text. The British Museum (Natural History), where abbreviated, is given as BMNH. In listing localities, co-ordinates are given for those not included in the gazetteer of the *Times Atlas*, vol. IV, 1958 edition.

METHODS

CHARACTERS USED

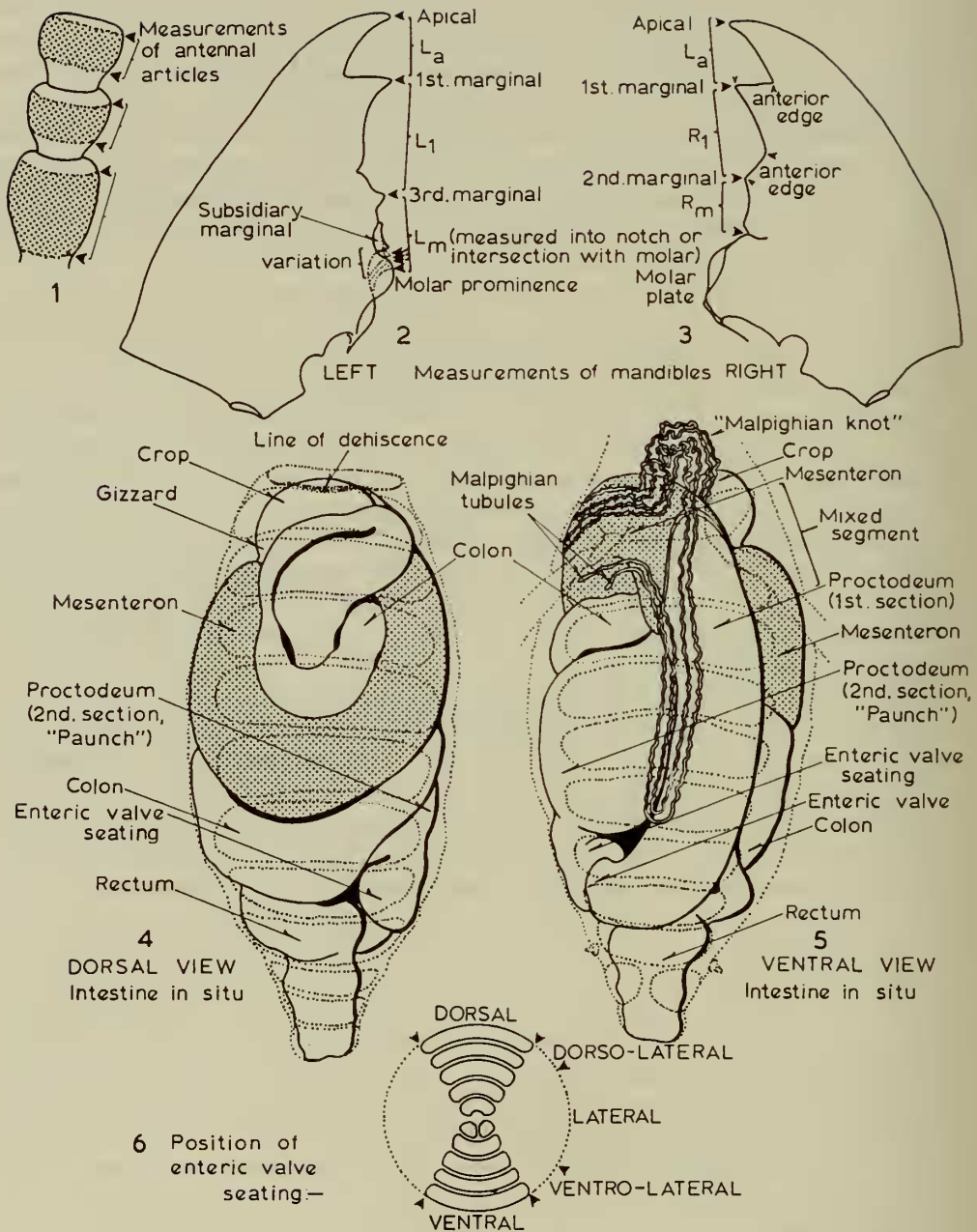
In attempting a comprehensive study of a group previously almost unknown, a careful search for suitable characters has had to be made. In the imago caste most of the more prominent external features have been used or illustrated before. However, some features have been found more important than previously recognized, and the value of some small details of structure more fully realized. The mandibles of both imago and worker castes have been subjected to detailed measurements. A small subsidiary marginal tooth on the left mandible, between and behind the third marginal and the molar prominence has been found to provide an important generic character. Silvestri (1913-14) illustrated the imaginal meso- and metanota but was only interested in the shape of their hind margins. These are of little taxo-

nomic value, but the width of the narrowest part between the wing processes of both nota is important. The presence or absence of a dark sclerotized suture at this point, the internal attachment of the oblique lateral dorsal muscles, is a further character. The 'medial frons spot' of Fuller (1925) lies immediately in front of the fontanelle and is the attachment of the medial muscle of the labrum. It is sometimes raised or depressed, and will be referred to simply as the medial spot. A pair of crescent-shaped or semicircular smooth marks between the ocelli and the posterior margin of the postclypeus were named 'antennal organs' by Holmgren (1909). Whatever their morphological origins, this name seems confusing and they will be referred to here as frontal marks. The antennae always have 15 articles in imagos and 13 in workers.

A considerable range of measurements of both imago and worker castes has been undertaken. These will be referred to again in the sections on multivariate methods. Although the analyses of measurements were done first, they are described after the multivariate similarity study based on coded characters. This is done because the latter follows on more naturally from the description of the non-measured characters. In listing measurements in the species descriptions, the limits of the range are rounded off to two decimal places. Where more than two specimens were measured a mean value was calculated and when measured series numbered five or more specimens the standard deviation is also given. These calculated values are given to three places of decimals. Where the rounded figures for the range coincide they are omitted and only the mean given. A single figure in the range column indicates invariance in the character for the specimens measured, in which case no mean is given.

In the worker caste a new set of characters based on features of internal anatomy is used. The existence of a histologically mixed segment in the digestive tract at the junction of the mid-gut and the hind-gut in the worker castes of the Termitidae was first demonstrated by Sutherland (1934). This author was also led by the appearance of its spiny armature to assume that the enteric valve functioned as a second 'gizzard'. The enteric valve is found in all termites where the first part of the hind gut enters or connects with the large pouch of the second, posterior part, sometimes referred to as the 'large intestine'. Grassé and Noirot (1954) studied in more detail the anatomy of the mixed segment and the enteric valve of a number of Termitidae, and pointed out the value of these characters in the systematics of the group. The differences in intestinal anatomy led them to propose separating certain genera in a new subfamily, the Apicotermitinae. Noirot and Kovoov (1958) carried the investigation of the gut in the Termitinae further and discussed its phylogenetic implications. Recently Noirot (1966) has included descriptions of the gut of the worker in describing two new Amitermitinae. Noirot and Noirot-Timotheé (1969) summarized the available information on the intestine of all termite families and Kovoov (1969) has carried out a more detailed study of the Nasutitermitinae that confirms the great importance of these characters in interpreting the phylogeny.

The detailed anatomy of the gut has not previously been investigated in the soldierless termites, but it forms an indispensable part of this revision. There is



FIGS 1-6. Details of some characters used. 1-3, antennal and mandible measurements; 4 & 5, worker caste abdomen-layout of intestine in situ; 6, meaning of terms used in description of enteric valve seating.

great variation in the length of the mesenteric overlap with the proctodeum, that is, the mixed segment, and its position related to that of the malpighian tubules provides both generic and specific characters. The enteric valve has a highly variable degree of armature and development and again provides both generic and specific characters. Its attachment to the pouch of the posterior part of the hind gut is modified in some genera by the development of part of the pouch into a tubular neck terminating in a more or less bilobed or trilobed valve-seating. This is usually visible through the body wall of an unopened worker termite, and its position is determined by the length and coiling of the various parts of the gut. The position of this structure can be stated relative to adjacent sternites or tergites and so provides a further useful character (Text-fig. 6). In some species the 'lobes' of the valve seating are developed into distinctive diverticula. Although some of these features can often be seen through the body wall, it is usually better to sacrifice a specimen to see them clearly. To examine the armature of the enteric valve a dissection and slide preparation are essential. Finding these structures and dissecting them out is not always easy and a more detailed description of the gut is needed. A diagram of dorsal and ventral views of a typical worker termite of this group is given in Text-figs 4 & 5. In dorsal view the long oesophagus traverses the narrow thoracic segments to open into the sac-like crop with the relatively feebly developed gizzard at its distal end. This is found beneath the foremost abdominal tergites and rests above and in front of one or two coils of the narrow part of the hind-gut. The wide and thicker-walled mid-gut (mesenteron) leads from the gizzard at first backwards on the left hand side in a loop round the outside of the coil of hind-gut (proctodeum) passing forwards and downwards on the right towards the ventral side. Viewed from the ventral side the mid-gut appears on the left leading forwards and across the front of the abdomen, just behind the posterior pair of legs. The loop of the gut passes across to the right, and the junction with the hind-gut is found in this region. The thin-walled hind-gut passes down the right hand side of the abdomen, and at the distal end crosses over to the left. Here it narrows to enter the enteric valve or passes round to the left lateral or dorsal side before reaching the valve, according to the proportions of the various parts of the gut. The pouch of the proctodeum beyond the enteric valve leads forward again to the coil within the mesenteric loop, and thence beneath this loop down the dorsal side to the dilated rectum. The junction between mid- and hind-gut may be simple, or overlapping as already stated to form a mixed segment of variable length. The four malpighian tubules severally enter the inner side of the mid-gut on the left in ventral view. They first loop backwards over the second pouch of the hind-gut and then pass forwards over the mixed segment into a tangled knot, which often extends into the distal part of the thorax under the hind coxae. This structure will be referred to as the 'malpighian knot'. From the malpighian knot the tubules spread out over the mid-gut and gradually become thinner to their ends, which loop back over the mixed segment and other parts of the gut. The function of the malpighian knot is unknown but it serves as a useful landmark in measuring the development of the mixed segment and as a recognition feature for this group of termites. No other group has the gut coiled in this precise way, which is thus

absolutely characteristic of the soldierless termites in Africa. The mixed segment, when present, always consists of a single extension of the mid-gut around the inner curve of the loop, with a corresponding extension of hind-gut round the outer curve. This is the reverse of all other groups, and will be discussed further in the section on phylogeny.

The dissection of the worker caste to obtain a clearer view of these structures is a simple matter. All that is needed is to pinch up the body wall of the ventral side near the hind coxae with fine forceps, and to tear it back towards the rectum. The pleural membranes rupture more or less evenly leaving the gut exposed. The ventral nerve cord and any residual muscle coats can then be picked off very quickly.

The other structure requiring more detailed description is the enteric valve. Its position has already been indicated. It can be dissected out by gripping the pouch beyond the valve seating, and the first part of the proctodeum anterior to the valve, with forceps. The valve can then be gently pulled out of its seating and detached from the proctodeum as a roughly conical stump with the valve armature inside its truncated apex. Repeated gentle pressure will expel the contents, and the valve can be mounted whole and cleared in one operation. For this purpose the variant of Gum chloral commonly known as 'Swan's Berlese' has proved completely satisfactory. The armature is easier to see if the valve is slit down one side with a fine blade and opened out, as shown in many of the plates. The valve, as described by Grassé and Noirot (*loc. cit.*) consists of longitudinal rounded ridges or cushions ('bourrelets') which carry a variety of spines and sclerotizations. In some genera these are such as to render the term 'cushion' inappropriate, but it is used throughout this paper to indicate the homology of the parts and avoid confusing circumlocutions. In a few species the thin membranous wall between the cushions also shows small scales or carunculations that bear fringes of spicules of varying size. These can usually only be seen at high magnifications with phase contrast illumination, and are not therefore intended as key or diagnostic characters except when very conspicuous. However they are of phylogenetic interest and so are included in descriptions and used for multivariate similarity studies. For the latter purpose, it was necessary to express the variation of each character in coded form, as dichotomies, multi-state qualitative characters, or as ranked or continuous quantitatives (measurements). The similarity analysis utilized species as O.T.U's with the objective of clarifying generic groupings. In theory, the characters are used without prior weighting, but it is inevitable in the process of coding that the logical structure of certain 'gross' characters necessitates their breakdown into a number of smaller units. This results in some centres of anatomical variation being represented by many more or less independent characters and so being weighted in the overall consideration of phenetic affinity. Such weighting seems intuitively to be natural, and might even to some extent be thought to reflect genetic complexity though there is of course no way of assessing this at present. An example of such a feature is the enteric valve in which 34 coded characters were required to express its variations in form. On the other hand some characters, such as the length of the mixed segment, appear to be under-represented because they do not lend themselves readily to logical breakdown. This feature is probably of considerable

adaptive importance, and where widely and consistently different is a useful character delimiting genera. Without deliberate weighting by arbitrary subdivision it only produced two coded characters, one alternative and one ranked quantitative. This may be an argument for the coding of all characters as dichotomies. Colour characters were treated quantitatively rather than qualitatively since in these termites colour is only a matter of progressive sclerotization and ranges from white to black through yellow and brown. In an earlier work (Sands, 1965) an arbitrarily decided scale of intensity employing 12 terms was used, and the same procedure was followed here. It was a simple matter to give these numerical values on the assumption that dark brown is more similar to brownish black than is pale brown. In a situation where different pigments are found, a qualitative treatment would be required but in the present case the quantitative approach seemed most appropriate.

Measurements of various body parts of both imago and worker castes were also included in the list of characters. An attempt was made to avoid excessive weighting of the general size factor by employing only those measurements that received large positive or negative loadings in principal components and canonical variates analysis. These are discussed in more detail in a later section. Multivariate methods of handling large numbers of measurements or attributes of organisms have been known for several decades and described in several textbooks (Kendall, 1957; Harman, 1960; Cooley & Lohnes, 1964; and Seal, 1964).

MULTIVARIATE SIMILARITY ANALYSIS

In recent years many taxonomic works have been published that make use of these methods and they have come to be recognized as a regular part of the technical armoury of the systematist. For this reason no list of references to individual papers is given apart from the textbooks mentioned above.

A total of 99 coded numerical characters was used for multivariate analysis by means of the classification programme (CLASP) devised by J. C. Gower on the basis of a method originally suggested by P. A. Sneath. It was carried out on the Orion Computer at Rothamsted Experimental Station, Harpenden, Herts. The list of characters is given below:

QUALITATIVES:

(i) *Alternatives*

- (1) Shape of posterior margin of imago head capsule
- (2) Shape of posterior margin of imago postclypeus
- (3) Pilosity of imago head capsule; presence or absence of a 'pelt'
- (4) Thickening of mesonotum between wing processes of imago present or absent
- (5) Thickening of metanotum between wing processes of imago present or absent
- (6) Median 'suture' of imago postclypeus present or absent
- (7) Frontal marks of imago head capsule depressed or flat

- (8) Pilosity of imago head capsule sparse, fine or inconspicuous, or more numerous and coarser
- (9) 'Abdominal dehiscence' in worker caste present or absent
- (10) Mixed segment of worker gut with or without inflated section at distal end
- (11-14) Enteric valve of worker gut: sclerotization of cushions present or absent (each of four independent positions)
- (15-18) Enteric valve: position of spines of main armature on cushions, proximal third, present or absent. ('Main armature' refers to scales or spines at least one place higher in rank under characters 88-91 than remainder. If spines uniform then all scored zero here)
- (19-22) Enteric valve: spines of main armature present or absent in mesal third
- (23-26) Enteric valve: spines of main armature present or absent in distal third
- (27) Enteric valve: membranous wall between and beyond cushions smooth, or carunculate or scaly
- (ii) *Multi-state qualitative*
- (28) Fontanelle of imago: shape; circular, short oval or elongated
- (29) Fontanelle of imago: level; depressed, flat, or slightly raised
- (30) Fontanelle of imago: size; vestigial, less than ocellus or more than ocellus
- (31) Medial spot of imago (i.e., small spot just anterior to fontanelle); shape (as above)
- (32) Medial spot of imago: level as above
- (33) Medial spot of imago: size; less than, equal to, or more than fontanelle
- (34) Frontal marks of imago (between ocelli and postclypeus); shape, indistinct or vestigial, crescent-shaped, or semicircular

QUANTITATIVE:

- (i) *Continuous variables* (measurements)
- (35) Imago: width of head capsule across compound eyes (W)
- (36) Imago: least diameter of ocellus (O_w)
- (37) Imago: greatest diameter of ocellus (O_1)
- (38) Imago: distance ocellus to compound eye (O-E)
- (39) Imago: length of postclypeus (maximum) (Pcl)
- (40) Imago: length of antennal article 3 (III) (Text-fig. 1)
- (41) Imago: length of antennal article 4 (IV)
- (42) Imago: left mandible, distance from apical to first marginal tooth (L_A) (Text-fig. 2)
- (43) Imago: left mandible, distance from first to third marginal (L_1)
- (44) Imago: left mandible, distance from third marginal to end of subsidiary tooth (L_m)
- (45) Imago: right mandible, distance from apical to first marginal tooth (R_A) (Text-fig. 3)
- (46) Imago: right mandible, distance from first to second marginal (R_1)
- (47) Imago: right mandible, distance from second marginal to notch between it and the molar plate (R_m)

- (48) Imago: width at narrowest part of mesonotum between wing processes (M)
- (49) Imago: width at narrowest part of metanotum between wing processes (N)
- (50) Worker: width of head capsule (W)
- (51) Worker: width of fore tibia (T_w)
- (52) Worker: length of fore tibia (T_1)
- (53) Worker: length of postclypeus (Pcl)
- (54) Worker: left mandible, distance from apical to first marginal tooth (L_A)
- (55) Worker: left mandible, distance from first to third marginal (L_1)
- (56) Worker: left mandible, distance from third marginal to end of subsidiary tooth (L_m)
- (57) Worker: right mandible, distance from apical to first marginal tooth (R_A)
- (58) Worker: right mandible, distance from first to second marginal (R_1)
- (59) Worker: right mandible, distance from second marginal to notch between it and the molar plate (R_m)

(ii) *Ranked quantitatives*

- (60) Imago: left mandible, state of subsidiary tooth
- (61) Imago: fore tibia, state of third apical spur
- (62) Imago: head capsule colour
- (63) Imago: postclypeus colour
- (64) Imago: colour of ocellar patch or streak
- (65) Imago: fontanelle colour
- (66) Imago: medial spot colour
- (67) Imago: colour of middle articles of antenna (VIII, IX, X)
- (68) Imago: colour of frontal marks
- (69) Imago: femora colour
- (70) Imago: tibiae colour
- (71) Imago: colour of tarsi
- (72) Imago: colour of abdominal tergites
- (73) Imago: dorsal abdominal stigmata colour
- (74) Imago: abdominal sternites, colour of lateral parts
- (75) Imago: abdominal sternites, colour of middle parts
- (76) Imago: colour of ventral abdominal stigmata
- (77) Imago: colour of cerci
- (78) Worker: left mandible; state of subsidiary tooth
- (79) Worker: fore tibia; state of third apical spur
- (80) Enteric valve: position of valve seat in unopened worker abdomen (Text-fig. 6)
- (81) Enteric valve: presence or length of neck separating valve seat from rest of second pouch or proctodeum
- (82) Enteric valve: presence or size of third (inner) lobe of valve seat
- (83) Enteric valve: size of two outer lobes of valve seat
- (84-87) Enteric valve: condition of cushions, retracted, produced, elongated, or extreme, for four independent positions

- (88-91) Enteric valve main armature, scale or spine development (reticulated scaly, minute, small, pronounced, very elongated)
- (92-95) Enteric valve main armature, spine numbers (0-10, 10+ to 20, 20+ to 30, 30+ to 40, no comparison if spines absent)
- (96) Enteric valve: presence or size of spicules on wall between or beyond cushions
- (97) Length of mixed segment of worker gut, relative to position of Malpighian knot
- (98) Worker: colour of head capsule
- (99) Worker: colour of head capsule pilosity

The CLASP programme provides for the computation of a matrix of coefficients of similarity between all the species, such that, as described by Sheals (1964):

$$S_{ij} = \frac{S_1 + S_2 + S_3 \dots S_k}{K} \quad (1)$$

where i and j refer to the OTU's being compared (in this case, species) and $S_1, S_2 \dots S_k$ are the similarities between them for each of the characters used, to the total K of characters for which comparisons are made. For qualitative characters S is scored on a match/mismatch basis, for a match $S = 1$ and a mismatch, $S = 0$. Similarity for quantitative characters is calculated by:

$$S_{ij} = 1 - \frac{|x_i - x_j|}{r} \quad (2)$$

where x_i, x_j are the ranked or continuous measurements, and r is the total range of the character in all of the taxa. The similarity coefficient S_{ij} between any two species thus rates a value between 0 and 1, but is presented as a percentage which is referred to as the *phenon* or *phenetic* level, or level of similarity. By the CLASP programme the matrix of similarity coefficients was first examined using the method of single-linkage cluster analysis. Every member of a group of species is similar to some other member at a phenetic level greater than L but similar to all non-members at phenetic levels less than or equal to L . L was first set to maximum (100%) phenon level and progressively decreased until all groups coalesced when sorting was terminated. A related form of clustering, median sorting, gave slightly different results as might be expected. Here after the selection of the first pair, the nearest neighbours of the mid point between them is taken rather than either member of the pair as in single linkage clustering. This to some extent reduces the likelihood of producing long chain clusters and seems intuitively more acceptable in considering relationships with more than one member when adding a new OTU to a cluster.

An alternative method of seeking structure in the similarity matrix is that named by Gower (1966), Principal Co-ordinates analysis. The matrix is first transformed by subtraction of row and column mean values from each corresponding matrix element added to the general mean of all elements, thus:

$$\alpha_{ij} = S_{ij} - \bar{S}_i - \bar{S}_j + \bar{S} \quad (3)$$

The Latent roots (eigenvalues) and vectors (eigenvectors) of the transformed matrix α are then found, scaling each vector so that the sum of squares of its elements equals its corresponding latent root. These vector elements provide the co-ordinates of the set of points representing OTU's (species) in relation to the orthogonal (uncorrelated) principal axes of the entire set, whilst preserving unaltered their taxonomic distances, defined by $\sqrt{2(\bar{r} - S_{ij})}$. The effect of the transformation to α is to remove the tendency for the first vector of the un-transformed similarity matrix to have more or less constant elements which allow for the mean value of all the elements of S .

In the present study, as is usual, it was found that the relationships between the points could be adequately summarized in a few dimensions by restricting consideration to vectors corresponding to the largest roots of α . This involved deciding where the variation represented by the smaller latent roots became insignificant and could be taken as residual. The first root took up 19% of the trace of α , the second 9%, and the third, 6%, together comprising only 34% of the total sum of squares. The next three roots together brought this to 48% of the trace. To include further dimensions graphically would make presentation of the results unwieldy and more difficult to interpret. Although collectively the residual dimensions account for slightly more than half the total information content of the transformed matrix, individually their contributions are small. They are therefore ignored although it is realized that there must then be some distortion of the relationships represented by the taxonomic distances which become approximations.

The matrix of similarity coefficients calculated for the majority of species is shown in Text-figs 7, 7a. Each species included is given a serial number indicating its position in the systematic order of this paper. Some few species were discovered, and one or two synonymies decided after the completion of the similarity analysis. It did not seem worthwhile to re-run the analysis for so small a number of changes and a few species are therefore omitted or appear twice.

The three methods used to examine the similarity matrix gave results that agree in general but differ in detail. Many published exercises in numerical taxonomy have been undertaken to test either the conclusions of an existing conventional classification, or the numerical methods themselves by comparison with it. In the present investigation no conventional classification existed, and attempts to develop one without the analysis of similarity were unsuccessful. Nevertheless where the groupings suggested by the numerical results appeared wrong by conventional standards, they have been adjusted to conform to the latter. The generic classification presented here therefore results from a blend of numerical and conventional methods.

Certain genera stand out clearly, the most distinctive being *Ateuchotermes* (serial numbers 36-42 inclusive) which is separated in both types of cluster analysis (Text-figs 8 & 9) by a wide gap from its nearest neighbours. The species of this genus all unite above 88% phenon level apart from *A. tranquillus* (Silvestri) (42). At the time of the analysis this species was represented by incomplete material and many test comparisons could not be made. Although separated by the cluster analyses, it was placed close to its congeners in several dimensions of the principal co-ordinates

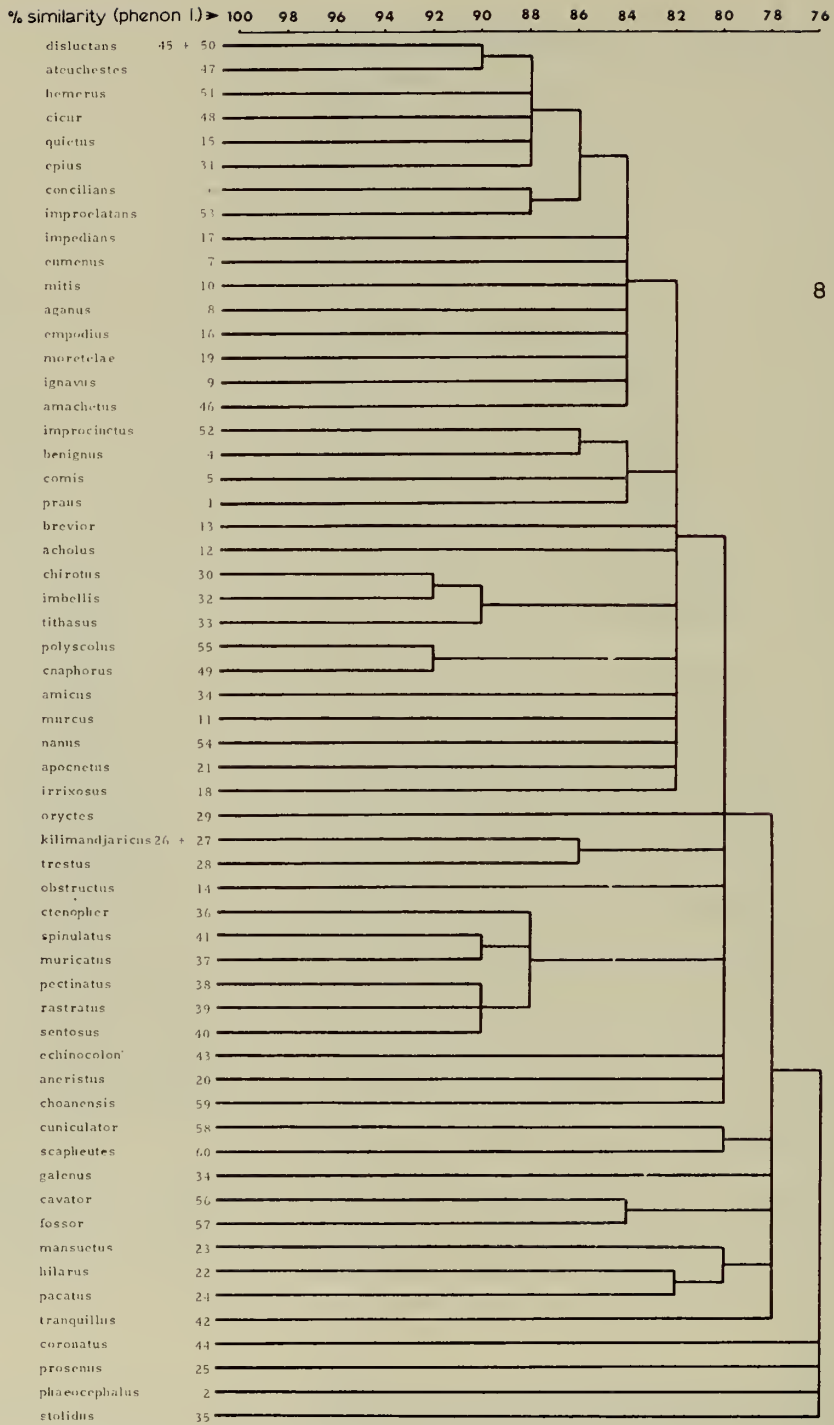


FIG. 8. Dendrogram showing phenetic relationships between species as indicated by single linkage cluster analysis.

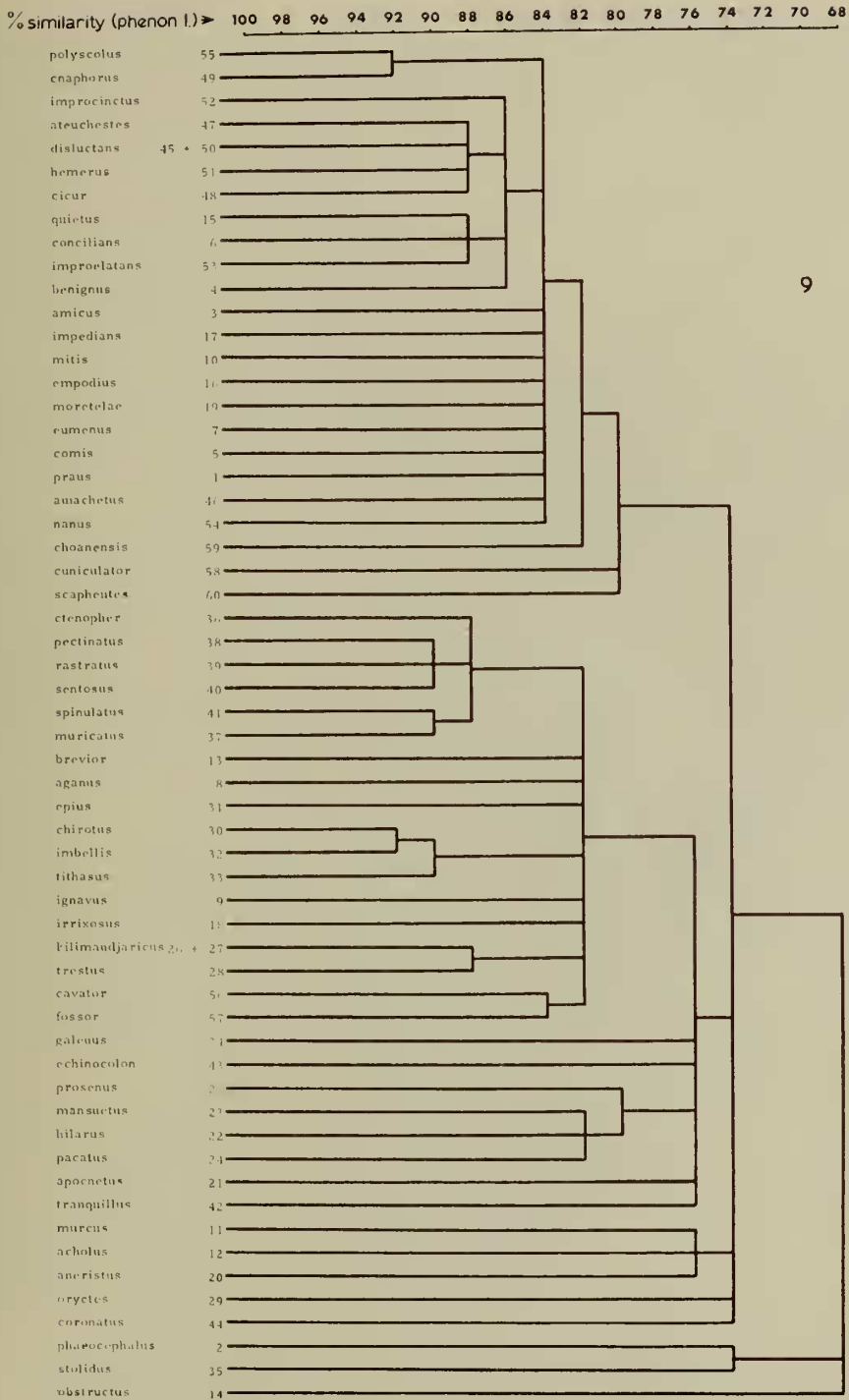


FIG. 9. Dendrogram showing phenetic relationships between species as indicated by median sorting.

analysis. Further material received later confirmed its membership of the genus. The position of *Ateuchotermes* is shown clearly in the three-dimensional graphs of the first six eigenvectors. All these were plotted as part of computer output, but the diagrams have been modified in various ways to enhance their visual impact. Vectors 1, 2 and 3 have been converted into a 'glass box' diagram (Text-fig. 10) with floors dividing the total range of vector 3 into four equal parts. Co-ordinates of vectors 1 and 2 are drawn in full on the last floor through which the stem of vector 3 passes before reaching the species point. From the last floor to the species point the stem is twice its lower thickness. Where the terminal part of a stem is hidden by the floor above it is drawn broken. The vector 2 shadow lines on the base plate help in spotting the origin of points arising from clumps on vectors 1 and 2. This type of diagram has been used effectively with fewer points in smaller analyses but is too complicated to be of much help in interpreting these results. Accordingly all other three-dimensional graphs have only been modified by adding their basal co-ordinates, which reverse direction about the zero value of each vector. The rest of the first six vectors have been plotted in the combinations 4, 5, 6; 1, 3, 5 and 2, 4, 6 in Text-figs 11, 12 & 13. This enables the relationships of species and genera to be visualized more clearly than would be possible in a single diagram. In the graph of vectors 1, 3, 5 the monotypic genera have been marked distinctively. Some species show up as more distinct from the main cloud of points in certain dimensions rather than others. An example is the monotypic genus *Adynatotermes* (19) which is distinct on vector diagrams 1, 3, 5 and 4, 5, 6. In other dimensions it is not far from the large loose group of points representing the genera *Astalotermes* and *Anenteotermes*, and it falls among them in both cluster analyses.

The distribution of points along the principal axes of the multivariate cloud represented by vectors 2, 4 and 6 seems to be more even than on vectors 1, 3 and 5, the latter combination producing the clearest indication of clustering. It is therefore used, with appropriate markings, in the introductory sections to successive genera to indicate the positions of their respective clusters and to compare them with those derived from the canonical variates analysis. In an analysis of the 'Q'-type such as the principal co-ordinates, the contributions of individual characters to the total variance represented by successive latent roots cannot readily be assessed as they can in an 'R'-type study. Thus the reasons for differences of dispersion along the principal axes remain unknown.

Other genera that stand out clearly in the cluster analyses are *Alyscotermes* (26-28) which is separated by a phenon gap of 6% from its relatives, and *Aderitotermes* (56-57). Three species of *Acholotermes* (30, 32, 33) come out together in both cluster analyses, but the fourth species (31) is variously separated from them. This is because its nearest neighbours are members of *Anenteotermes* as can be seen from the vector diagrams. It is located on the same side of the larger cluster as the other members of its genus, and a conventional decision places it differently from the numerical methods. It has a short mixed segment like the other *Acholotermes*, not a long one like *Anenteotermes*, and is possibly a transitional species.

In the single linkage clustering three species of *Astratotermes* (22-24) form a group, and median sorting adds a fourth (25), while a fifth (21) comes in at the next general

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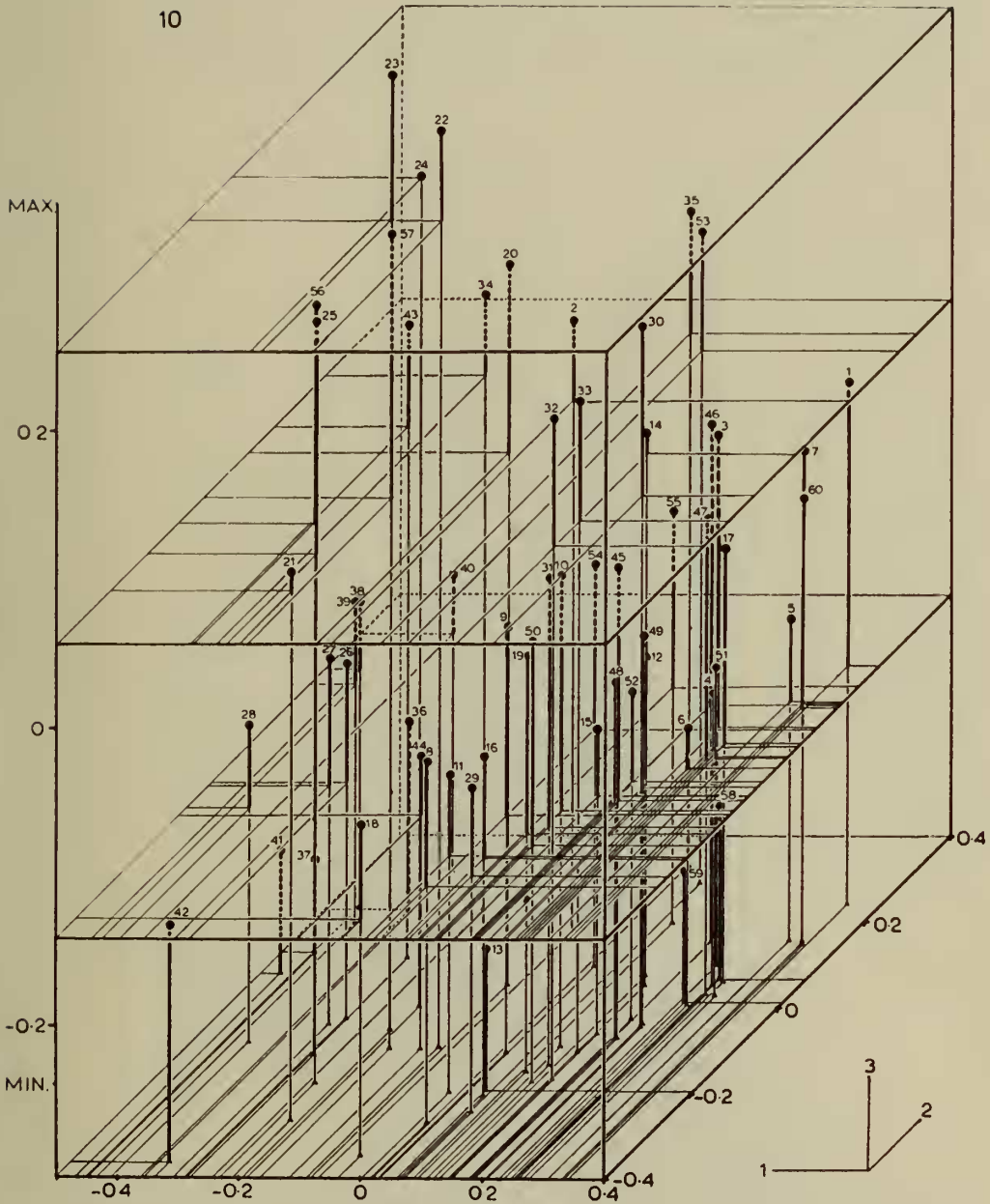


FIG. 10. Three-dimensional graph of principal co-ordinates analysis-plot of eigenvectors corresponding to latent roots 1, 2 & 3 in a 'glass box' diagram. Species-points are numbered to correspond with Text-figs 7-9.

additive level. The last species (20) is not clearly linked with the rest by cluster analysis but on vector diagrams 1, 2, 3 and 1, 3, 5 stands nearby. Its separation and that of (21) arises from their positions at lower levels shown on vector diagrams 4, 5, 6 and 2, 4, 6.

The genera *Adaioprotermes*, *Anentcotermes* and *Astalotermes* were not very clearly

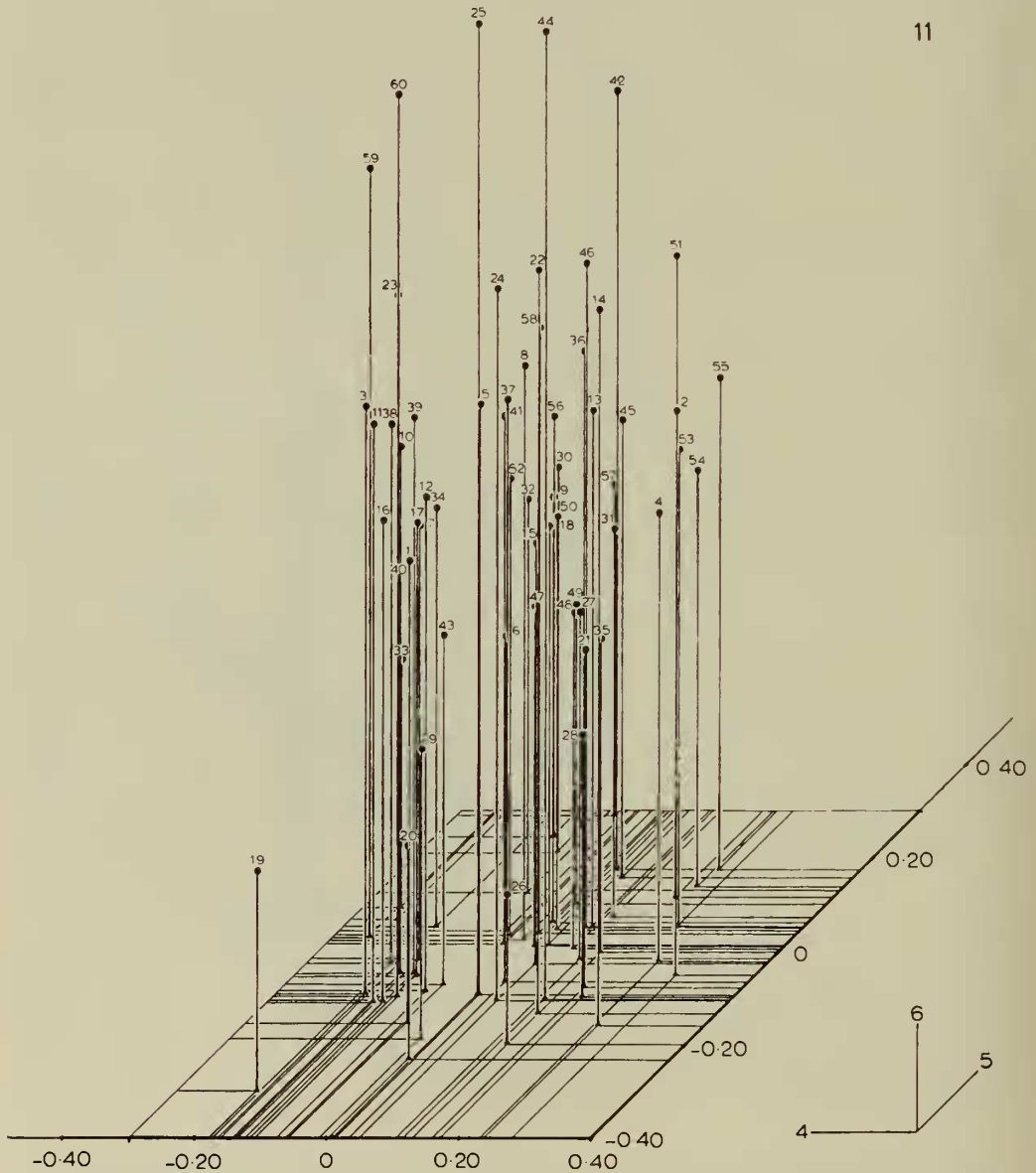


FIG. 11. Three-dimensional graph of principal co-ordinates analysis-plot of eigenvectors corresponding to latent roots 4, 5 & 6.

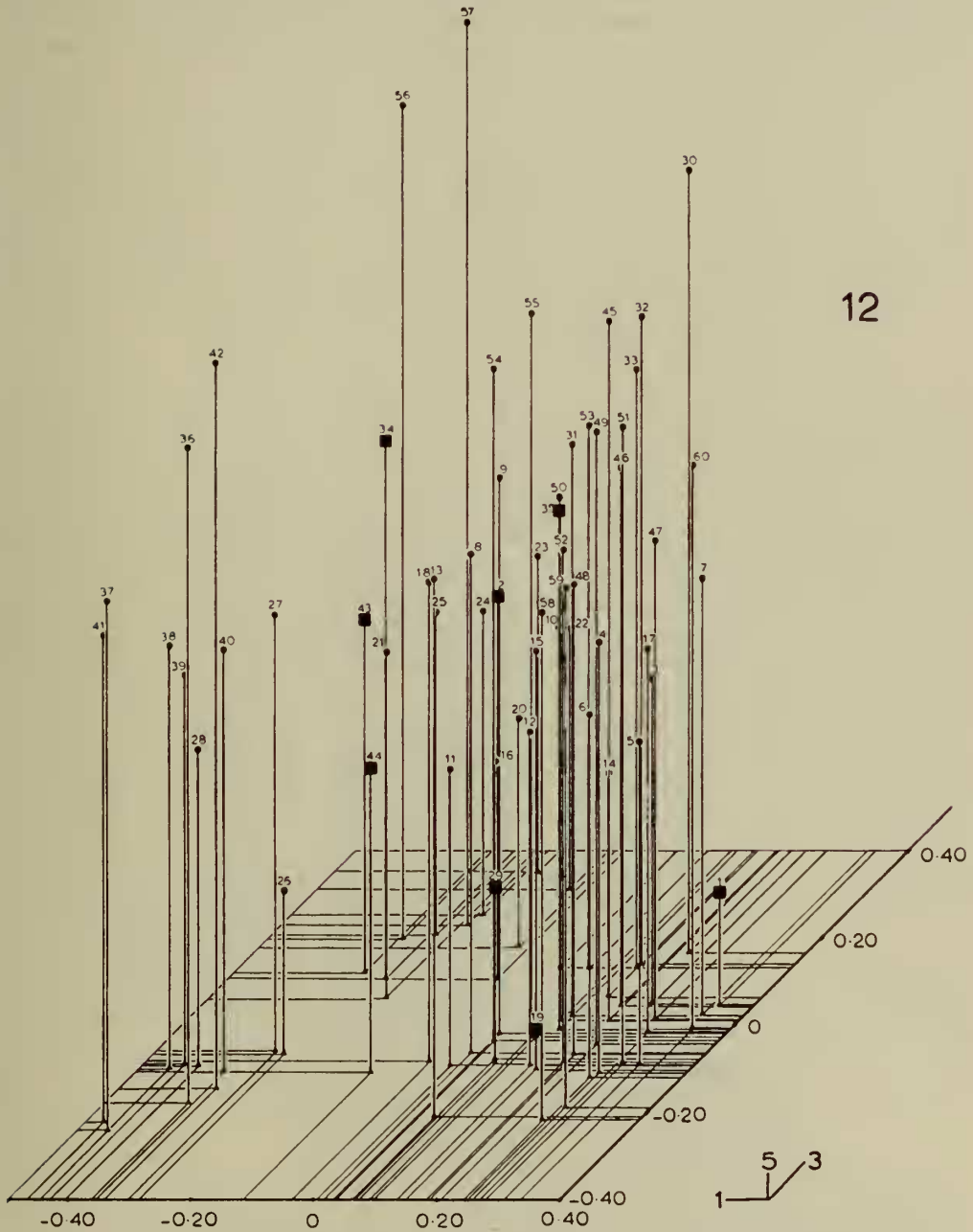


FIG. 12. Three-dimensional graph of principal co-ordinates analysis-plots of eigenvectors corresponding to latent roots 1, 3 & 5. Monotypic genera marked with large black squares.

distinguished by any numerical methods and the reason for this is obvious from the vector diagrams. As already mentioned they form a rather large loose cluster with no clear divisions. *Astalotermes* (3-18) occupies the 'lower' half of the cluster in the graphs of vectors 1, 2, 3 and 1, 3, 5 with little mingling, reflecting the largely

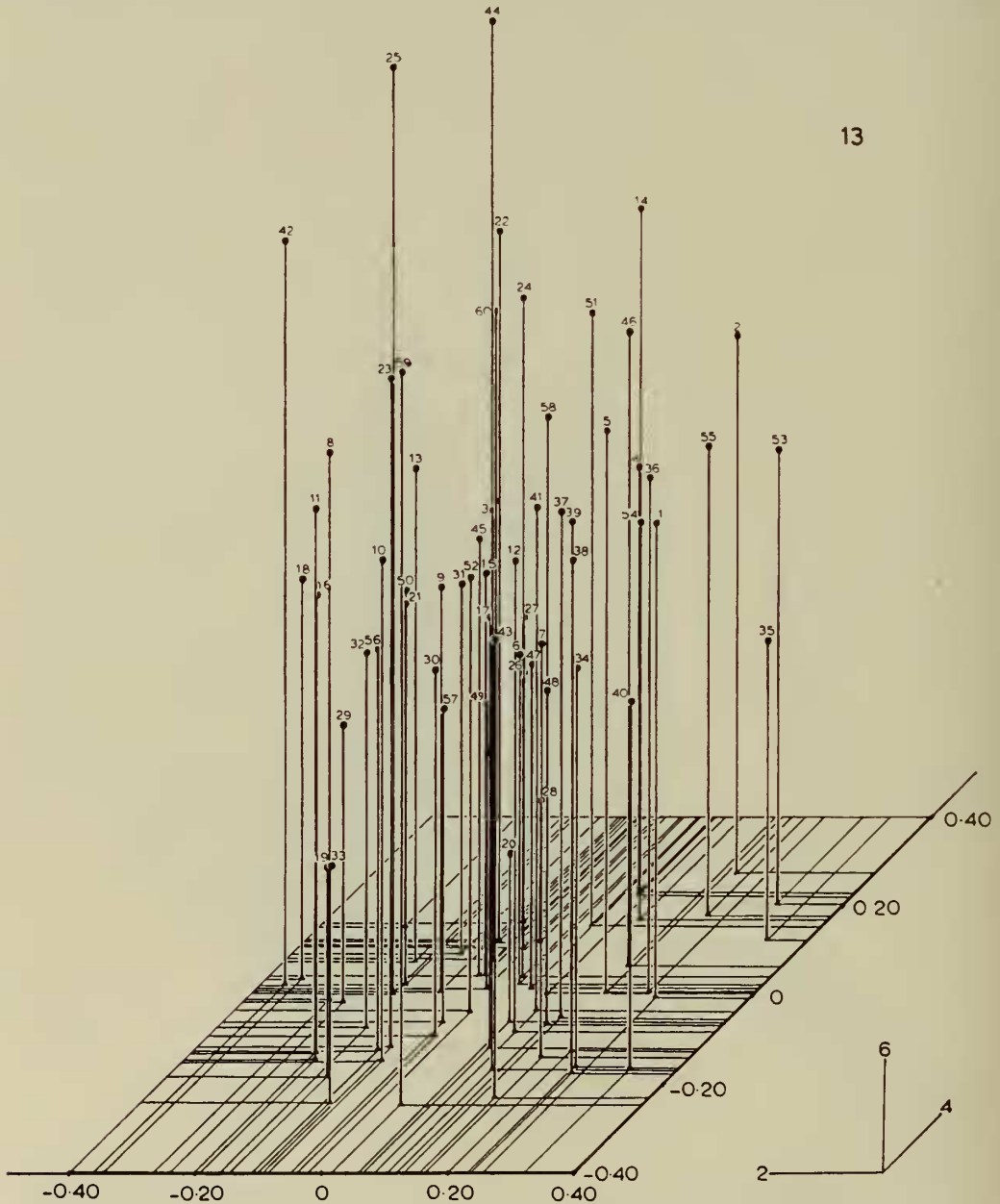


FIG. 13. Three-dimensional graph of principal co-ordinates analysis-plot of eigenvectors corresponding to latent roots 2, 4 & 6.

negative or low positive values of their corresponding elements of vectors 3 and 5. *Anenteotermes* (45-55) occupies the 'upper' half of the cluster having largely positive or low negative values in these vectors. *Adaiaphrotermes* forms a line of three points (58-60) to one side. The nearest neighbours of some species in each genus are in the adjoining genera, and this is accentuated by the close intermingling of the species of all three that occurs in other dimensions all of which contribute to the taxonomic similarities on which the cluster analyses are based. In these three genera which are generally similar, the intestinal characters clearly separate them on a conventional basis. *Astalotermes* has virtually no mesenteric overlap with the proctodeum, or mixed segment. In *Anenteotermes* there is a long mixed segment, also present in *Adaiaphrotermes*, but in the latter the mesenteron is dilated at its posterior end and the fore tibia has only two apical spurs. The relationships of the genera are discussed in more detail in the section on phylogeny.

MULTIVARIATE ANALYSES OF MEASUREMENTS

The shortage of other characters has led taxonomists to make increasing use of measurements in studying termites. However, this has developed very largely on a trial and error basis and a large number of differing measurements and ratios (indices) have been employed. Roonwal (1964) noted that 66 measurements and 34 indices had been published and suggested a further 22 and 19 respectively bringing the totals to 88 measurements and 53 ratios. He recognized that such numbers were impractical and advocated a selection of the 'more useful and sensitive characters' numbering 32 measurements and 18 indices 'for general use'. The method of assessing sensitivity was not indicated. There has been some published discussion on the numbers of individuals of any species or colony series that should be measured to obtain a representative sample for statistical purposes. Bouillon (1966) concluded that 6-10 specimens were sufficient. Variation within colonies of the soldierless termites was soon found to be slight, about 5% being the maximum range for either sex or caste. In these small termites accurate measurements of small features such as mandibular teeth are difficult to take. It was concluded from preliminary tests with common, well represented species, that for the purposes of the multivariate analyses it was adequate to measure one or two specimens of each caste from each colony.

One of the first applications of multivariate analysis to a taxonomic problem was made by Stroud (1953) using the complete centroid method of factor analysis (a close approximation to principal component analysis) to sets of measurements of the imago and soldier caste of *Kalotermes* species. Since then these methods have been applied in many other plant and animal groups, but not in termite systematics.

The purposes of principal component analysis used in taxonomic problems may be summarized as the extraction from a large body of primary data the smallest number of meaningful dimensions; to interpret these where possible in terms of recognizable characteristics, and to derive from their objective weightings a set of taxonomic indices giving the best discrimination of individuals. The clustering of individuals into groups can be examined, and misplaced specimens recognized.

Canonical variate analysis has similar purposes to principal component analysis, except that it requires all individuals to be assigned to taxa and each taxon to be represented by more than one specimen. The weighting of variables is then directed to those providing the best discrimination between the taxa.

Both types of analysis treat individuals or individual taxa as points in a hyper-space, their positions defined by the numerical values of all their measured variables. Both seek new sets of orthogonal (uncorrelated) co-ordinates corresponding to successive axes of maximum variation of the scatter-cloud of points. The difference between the two is that where principal component analysis is concerned with the dispersion of individuals, canonical variate analyses measures the dispersion of the ends of the mean vectors of the taxa. Thus the characters weighted by the two analyses will not necessarily be the same. However, there is likely to be a tendency for this to happen in a large body of data. Both analyses call for the extraction of the latent roots and vectors of a matrix. The vectors provide weighting coefficients by which the transformation of the variables (characters) to the new set of co-ordinates is achieved. In principal components either the variance-covariance matrix or the correlation matrix is used. In the latter case the variables are standardized, being expressed in standard deviation units with a variance of 1. This is the commoner procedure, and was employed here. In canonical variate analysis the 'between-taxa' and 'within-taxa' dispersion matrices are together used to compute a further matrix, of which the latent vectors give the required multiple discriminant functions.

The total number of latent roots and vectors produced is the same as the number of original variables. The size of successive latent roots indicates the proportion of the total variance of the matrix taken up by each of the new co-ordinates in turn. The number of roots, and hence the corresponding vectors, considered significant depends on their relative size. One convention recommended by Kaiser (1960) and Harman (1960) is to disregard roots smaller than 1.0. However, when using the analyses mainly for descriptive purposes, as here, it seemed more appropriate to examine the elements of the vectors to determine the point at which large weighting coefficients cease to be attached to new characters. This would suggest that little further significant information was being extracted.

It would also have been possible to carry out a principal component ('R'-type) analysis of a correlation matrix based on the coded character data described earlier. However, Gower (1966) pointed out that the 'Q'-type approach of principal coordinate analysis based on a similarity matrix is mathematically equivalent to the 'R'-type, but is computationally simpler and statistically more appropriate when many qualitative variates are included.

In order to arrive at an objective assessment of the taxonomic value of measurements to be used, several principal component and canonical variate (multiple discriminant) analyses were undertaken. More measurements of both imago and worker castes were made than were likely to be put to practical use, in the expectation that the analyses would pick out the most valuable. Some of those suggested by Roonwal were rejected because they are those of parts easily altered by distortion

due to drying, ageing, or feeding differences of specimens. Others were eliminated because they cannot be delimited by fixed points but depend upon the angle at which the specimen is held; others again are those of parts too often missing in all but freshly moulted specimens. The absence of the soldier reduced the numbers further. The input for the imago caste finally consisted of 25 measurements, and for the worker, 13. Some of these are listed in the previous section. The remainder were as follows: Imago: greatest diameter of compound eye, pronotum width, pronotum length, hind tibia length, width of postclypeus, length of antennal articles I, II, V and IX; Worker: pronotum width, length of hind tibia, and postclypeus width.

These measurements were recorded by means of an I.B.M. Port-a-punch on 40 alternate columns of special partially pre-punched 80 column-type cards, as microscope eyepiece graticule divisions. In this form they are already acceptable to some computer installations, but it was also easy to reproduce the data in the first 40 columns of standard cards by machine, and considerable savings of time in handling and preparation of input for computer processing resulted. Conversion to millimetre values, summarization of the data and calculation of complex ratios, as well as the more sophisticated techniques, were all able to proceed without the need for further transcription.

The measurements of the imago castes were subjected to two principal component analyses. The first used the raw data, and the second its logarithmic transformation. The purpose of the latter was partly to avoid any bias in the weighting of the characters arising from fairly large size differences among them (e.g. antennal articles or mandible measurements were often less than one-tenth head width or tibia length). In addition, it was desired to test the idea that the pattern of variation might be at least as well expressed by ratios as by linear functions of the variables. The weighting coefficients of the second analysis were almost identical with the first, suggesting that there was little likelihood of biased weightings arising from size differences. It also indicated the validity of interpreting the relationship between characters by complex ratios. This was particularly useful in the derivation of a set of taxonomic indices, since a positive character weighting could be interpreted by a multiplication and a negative weighting by division. The larger weighting coefficients of any vector tended to be rather similar in size. Because eigenvectors are scaled arbitrarily, it is the relative size of the elements that is important. Therefore in calculating taxonomic indices for practical use in keys, it was a sufficient rough approximation to use the raw measurements without the additional complication of weighting coefficients.

Since the two analyses of the imago were so nearly identical only the raw measurements were used for a principal component analysis of the worker caste. One further analysis of this type was undertaken in which the measurements of a single female imago and one worker from each nest-series were combined as representing a set of attributes of the colony. It was necessary to confine the choice of imago to one sex because there is a slight tendency for males to be smaller than females, and to mix them would have obscured the relationship between the variables. The purpose of this last analysis was to see whether it gave any clearer indication

of clustering and incidentally to find out whether any adaptive features of the same structures of one caste were expressed as dimensions of variation clearly independent of the other. In addition, by using only a selected part of the data, it provided a check on the validity of character weighting obtained from the other analyses.

In this combined analysis of the imago and worker characters the lowest correlations occurred, as expected, between those of different castes and present in only one of them. Imago antennal articles, for example, were weakly correlated with worker fore tibia width. Since these probably represent adaptations to totally

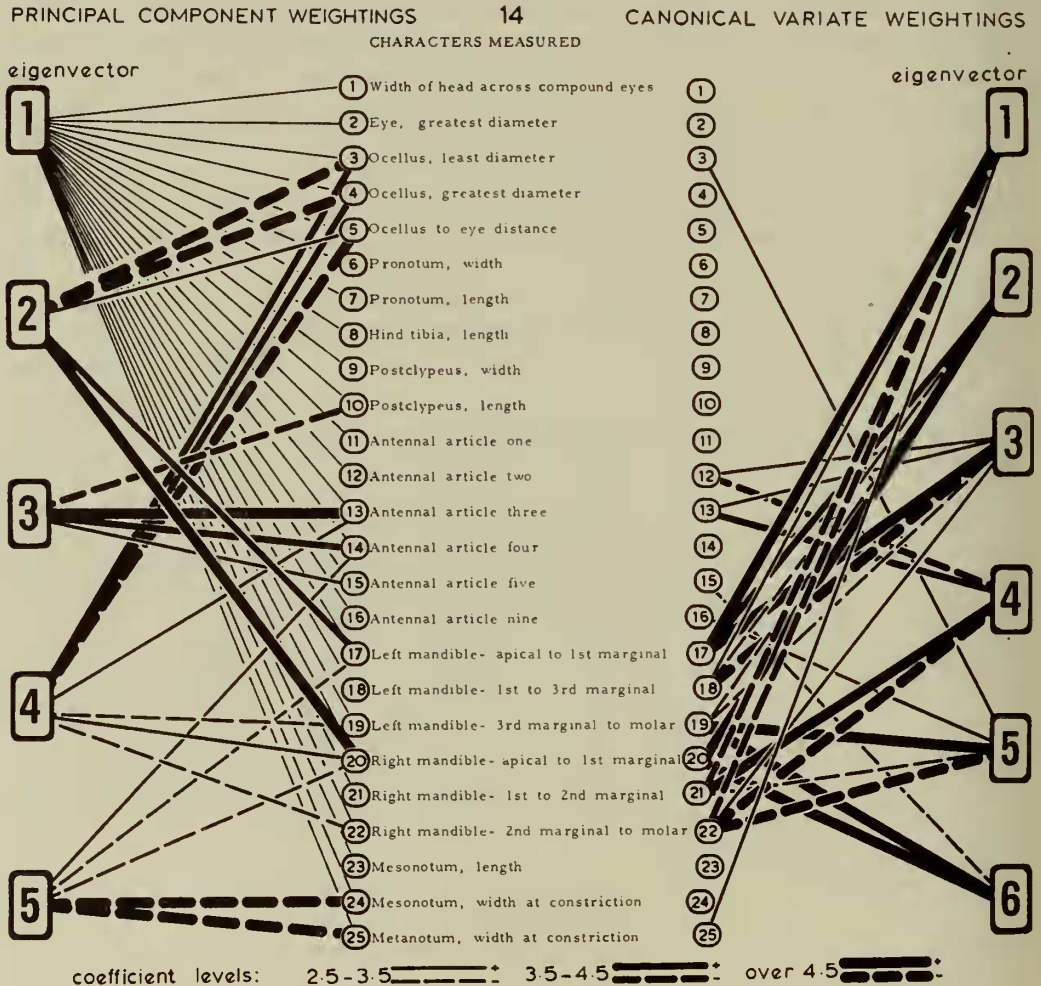


FIG. 14. Imago caste-weightings of measured characters obtained from two multivariate analyses, principal components and canonical variates. The weighting coefficients of eigenvector 1 of the principal component analysis were all less than 2.5 and closely similar in value.

different aspects of behaviour and environment their variation is unlikely to be closely linked, except by a general size factor. However, the correlations between corresponding characters of imagos and workers were sometimes lower than might be expected on the assumption that they are adapted to the same functions. The inter-caste correlations, expressed as percentages, are tabulated for the common characters of imago and worker as follows:

Head width	94·15
Pronotum width	87·38
Hind tibia length	91·84
Postclypeus width	90·46
Postclypeus length	74·17
Left mandible, apical to first marginal tooth	92·23
Left mandible, first to third marginal	88·47
Left mandible, third marginal to molar	76·09
Right mandible, apical to first marginal	91·14
Right mandible, first to second marginal	87·15
Right mandible, second marginal to molar	80·18

This table would seem to show that while the lengths of apical teeth of the

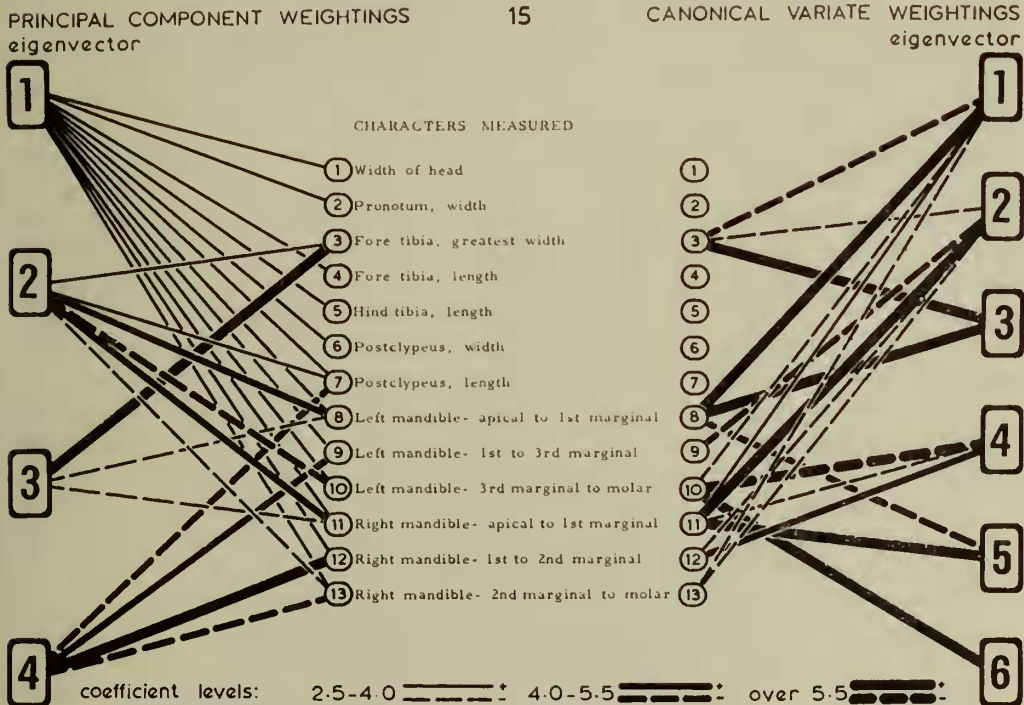


FIG. 15. Worker caste-weightings of measured characters obtained from two multivariate analyses as in 14. In the principal component analysis the weighting coefficient on character 3 in eigenvector 1 was about half the size of the rest.

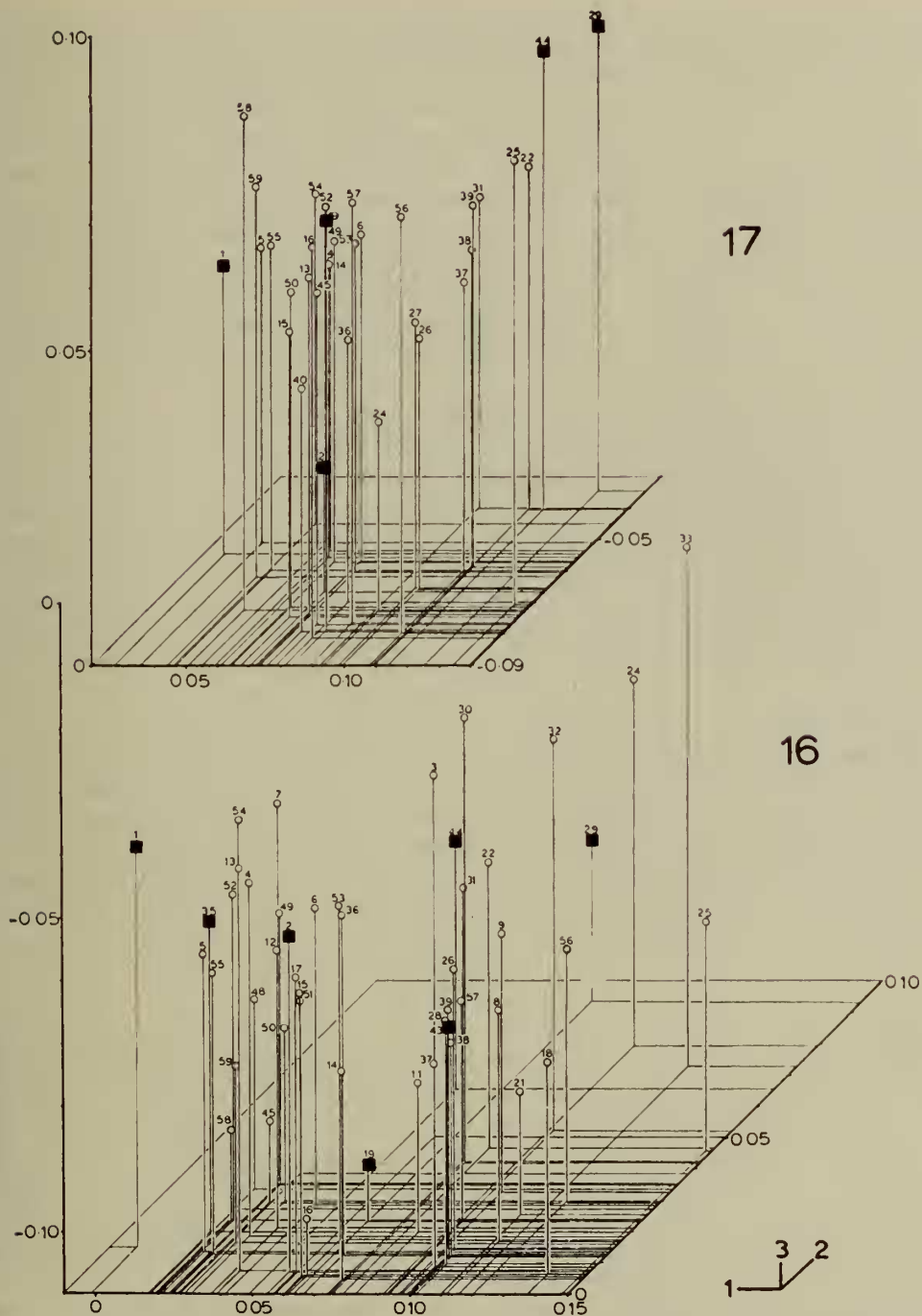
mandibles of both castes are closely correlated, there is a good deal of independent variation in the proportions of marginal and molar parts of the worker mandibles. These sections of the mandible are not merely more variable than those of the imago, but proportionately more variable than their own apical sections. It is not yet clear how to interpret this in terms of adaptation to feeding or other behaviour, and more detailed studies need to be made.

The length of the worker postclypeus is similarly less strongly correlated with that of the imago than might be expected. Since the postclypeus houses the cibarial dilator muscles it is probably associated with the pumping or manipulation of moistened soil particles. It is conceivable that this is associated in imagos with tunnelling to found a new colony and otherwise little used, whereas in the worker it must be used in a variety of ways throughout its life. The independent variation could be a response to different situations.

The independent dimensions of variation indicated by the correlation coefficients were also shown in the elements of the eigenvectors corresponding to the first five latent roots that together accounted for 89% of the trace of the correlation matrix. The first vector as usual consisted of largely similar elements, associated with a general size factor, and represented 76% of the variation. The second vector had its largest elements contrasting the apical teeth of the imago mandible with the molar measurements of workers. Other features given major importance by this vector were the worker apical teeth and the length of the imago postclypeus. The third and fourth vectors were mainly concerned with variation in characters only present in one caste or the other. It was not until the fifth vector that the small independent variation of the worker postclypeus received a weighting coefficient of any size, and here it was involved in a contrast with several characters of imago and worker mandibles. This vector corresponds to a latent root of less than 1.0 (0.7) representing only 1.8% of the variance. This brief account serves to show that the method may yield useful comparisons of homologous structures in different castes of social insects. The detailed figures of the analysis are not appropriate in this context, and the full data are retained for future reference at the BMNH.

The canonical variates analyses carried out separately on imago and worker castes demanded at least two representatives of each of the species included, and some consequently had to be left out. Instead of the 60 putative species represented in the foregoing analyses, the analysis of the imago covered 50, and that of the workers 34 species. Thus although the canonical variates gave some indication of the grouping of species into genera so far as this is shown by measurements they were necessarily incomplete. The larger weightings of these two analyses, although naturally with different numerical values, were attached to essentially the same set of characters as in the principal component analysis. This probably arose partly from the fact that many species were represented by small numbers of specimens and the dispersion of the ends of the mean vectors was thus closely related to that of the individuals. However, the combinations of character weightings in the eigenvectors differed slightly, suggesting differing emphasis on characters involved in clustering species and on those of greater value for generic discrimination.

The character weightings obtained from both principal component analyses and



FIGS 16 & 17. Three-dimensional graphs of canonical variates 1, 2 & 3. 16, Imago; 17, worker caste. Species-points numbered as in Text-figs 7-13, monotypic genera marked by solid squares.

canonical variate analyses are shown graphically for the imago and worker castes in Text-figs 14 & 15 respectively. These diagrams are intended to be self-explanatory and avoid the necessity for tables of figures. In the principal component analysis the weighting coefficients of the first eigenvector all tend to be similar in size, representing what in factor analysis is sometimes called a general factor, apparently related to the general size of the insect. All measurement characters will naturally contain a large element of closely correlated size variation and the first vector is often disregarded except to take one convenient measurement as a size indicator. In the present work the width of the head is used. In the worker diagram it is worth noting that character 3 carried a much lower weighting on the first vector, indicating an unusually large proportion of the variation independent of size. This reflects its importance as a taxonomic character and its interest as an adaptive feature.

The correlation matrices, the numerical values of the vectors, the component scores, and the canonical variates are not published in full to save space. Two-dimensional graphs of principal component scores are shown under the headings of individual genera where they are of interest in separating pairs of closely related species or indicating misidentifications. The first three canonical variates of imago and worker castes are used in the introduction of each genus to illustrate the clustering of species based on numerical characters for comparison with that of the principal co-ordinates. The positions of the species of each genus are shown by solid spots instead of circles. The monotypic genera are shown together in Text-figs 16 & 17.

TEXT-FIGURES

The termites have all been drawn with the aid of a camera lucida, from ethanol-preserved specimens immersed in ethanol. Two scales are used, the larger being twice the smaller. All illustrations of entire head capsules are on the smaller scale and all mandibles on the larger. Parts of the intestines of the worker caste are on either scale according to their relative size but the scale of any particular part is not altered between species on one page of illustrations. The only exceptions to the above are illustrations of the entire gut, which are on a third, lower scale.

PHYLOGENY

The description here of numerous new species and genera throws the existing classification somewhat out of balance. Similar undescribed complexes exist in other zoogeographical regions, and will, when described, add to this difficulty. The previously described species included in this study have hitherto been placed in the genus *Anoplotermes* of the subfamily Amitermitinae. This subfamily has included a considerable variety of forms, and habits ranging from soil-feeding, through wood- and detritus-feeding to harvesting grasses and foliage. Ahmad (1950) recognized four evolutionary series based primarily on the dentition of the imago and worker mandibles within the subfamily. He regarded the group that included *Anoplotermes* and *Speculitermes* as the most primitive, and in his hypothetical phylogenetic tree showed it branching off near the base of the main stem. The remaining groups he regarded as more closely related to one another as side

branches at a higher level. Thus the most significant division of the subfamily separated off the mainly soil- or litter-feeding forms which are characterized by an segment. This also applies to the other 'genus' mentioned by these authors, namely those species of african '*Anoplotermes*' known to them. In the latter group the enteric valve was stated to be unarmed.

One further genus has been described in the subfamily that does not fit the two main groups as defined above. Deligne & Pasteels (1969) give details of the intestine of *Labidotermes*. There is no mixed segment in this genus and the malpighian tubules are attached to the midgut. The enteric valve armature has only a single large tooth at the anterior end of each cushion. The worker mandibles are similar to those of the *Anoplotermes-Speculitermes* group.

indentation of the incisor edge of the left mandible separating the third marginal tooth from the first plus second. Ahmad considered the right mandible to be more specialized in the curved posterior edge of the second marginal, on the grounds that the 'primitive' condition had a straight cutting edge. In this he was influenced by its appearance in most of the otherwise primitive wood-feeding groups of termites. It should be noted, however, that in the primitive cockroaches, *Polyphaga* and *Cryptocercus*, as well as most of the rest of this group, the right second marginal has a convex anterior and concave posterior margin. In first instars of *Archotermopsis* the same applies, the tooth becoming straighter in adults. It seems probable that this straightening of the right second marginal tooth is an adaptation to feeding on fibrous materials that require shearing. This is supported by the same tooth in the soldier caste of some wood-feeding primitive forms. When the expression of the gene complex controlling mandible development switches to the piercing soldier function, the tooth reverts to the cockroach form. Thus it would seem that where such a tooth occurs in otherwise primitive species it is itself a retention of an unspecialized condition.

When Noirot & Noirot-Timothee (1969) came to consider the intestinal structure of the Amitermitinae they found two basic patterns. One is found in the group of genera including *Anoplotermes*, *Speculitermes* and *Eurytermes*. The gizzard lacks armature, the mesenteron overlaps with the proctodeum to form a mixed segment, and the malpighian tubules are attached separately within the epithelium of the mesenteron. The enteric valve is unarmed. The other type occurs in the rest of the subfamily with one or two exceptions. The mixed segment is always well developed, often with the termination of the mesenteron to some extent inflated. The first segment of the proctodeum is commonly dilated and the malpighian tubules are inserted, usually in pairs, on the mesenteric-proctodeal junction. The gizzard carries typical armature. Associated with this group also are the genera *Protohamitermes*, *Prohamitermes*, *Globitermes* and *Synhamitermes*, which differ only in that the malpighian tubules are carried on evaginations at the junction of mesenteron and proctodeum rather than directly attached. Thus apart from *Protohamitermes* these authors agree with the basic division postulated by Ahmad. The mandibles of the latter genus are primitive in form and show some general resemblance of shape to the other main branch. Its gut is one of the more specialized, and clearly indicates that its affinities are with the *Amitermes* branch although

diverging from very near its base. One difficulty in accepting this position has been thought to be its lack of a soldier caste. However, 'soldierlessness' is an adaptive character that could develop several times over; considering the rarity of soldiers in a number of groups this is perhaps not a serious obstacle.

Noirot and Noirot-Timotheé noted two exceptions to the above scheme. *Eburnitermes*, a monotypic genus described by Noirot (1966), was included by him in the Amitermitinae mainly on the basis of the similarity of the worker mandibles to *Eurytermes* and the soldier to those of the same group of genera. He pointed out the resemblance of the gut to that of the Apicotermitinae, particularly in the armature of the enteric valve and the short first segment of the proctodeum. The malpighian tubules are again attached some way up the midgut. There is no mixed segment. This also applies to the other 'genus' mentioned by these authors, namely those species of african '*Anoplotermes*' known to them. In the latter group the enteric valve was stated to be unarmed.

One further genus has been described in the subfamily that does not fit the two main groups as defined above. Deligne & Pasteels (1969) give details of the intestine of *Labidotermes*. There is no mixed segment in this genus and the malpighian tubules are attached to the midgut. The enteric valve armature has only a single large tooth at the anterior end of each cushion. The worker mandibles are similar to those of the *Anoplotermes-Speculitermes* group.

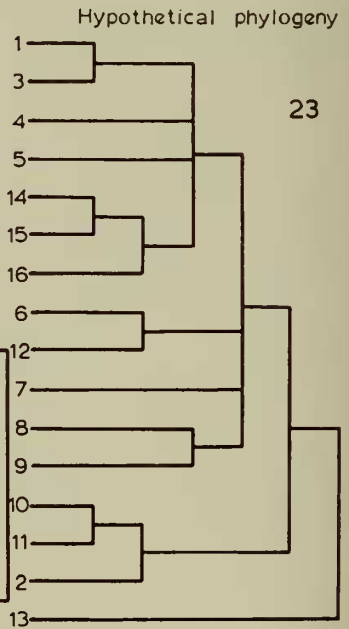
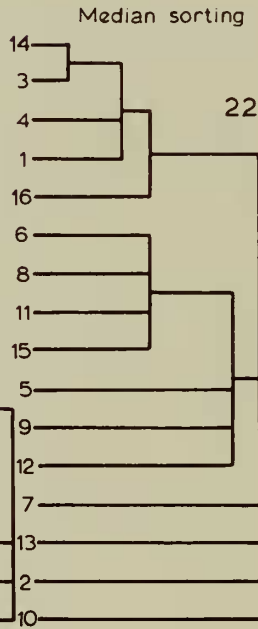
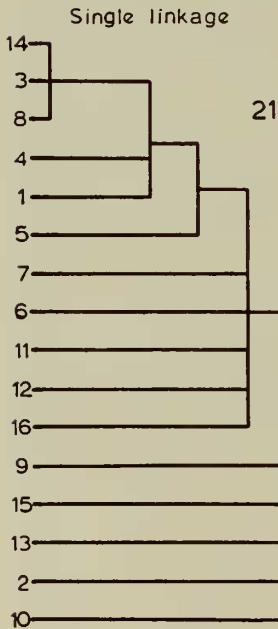
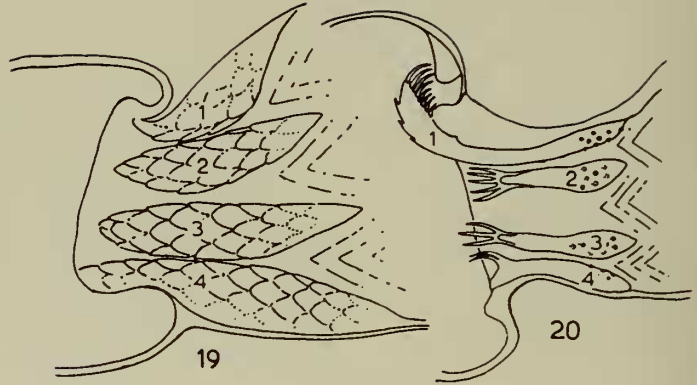
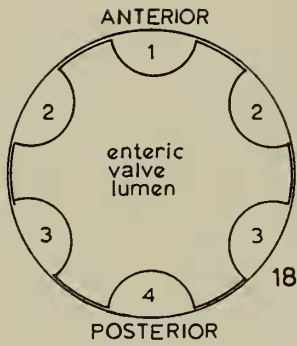
In a preceding section the layout of the gut of the african soldierless termites is described and an account given of its variations. Further details will be found in the introductory passages to genera and in species descriptions. The salient features are illustrated for all species. Within the group are found all stages in the development of the mesenteric overlap with the proctodeum from a simple transverse junction like those of *Eburnitermes* and *Labidotermes*, to elongated mixed segments with dilated ends. There are also all stages in the development of enteric valve armature from nothing at all to elaborate spines, hooks and sclerotizations everted through the valve opening. A similar though less extensive variety of forms has been seen in the Neotropical species of *Anoplotermes*. Thus the exceptions mentioned by Noirot and Noirot-Timotheé to the two divisions of the Amitermitinae are not separable by any sharp division from the first type in which the malpighian tubules are attached to the wall of the midgut. In addition in all these forms the gizzard is feebly developed. The other important character is only readily appreciated by examination of the layout of the gut in situ. Once uncoiled, the relative positions of its parts are displaced. In the first type of Amitermitinae where a mixed segment is found the extension of the mesenteron is always around the inner curve of the coil of the gut on the same side as the insertion of the malpighian tubules.

In the second group of Amitermitinae the extended part of the mesenteron forming the mixed segment is always around the outside of the loop of the gut on the opposite side to the malpighian tubules where these are attached at the anterior end of the proctodeum. A number of possible exceptions have been examined, such as *Prohamitermes*. Here the mesenteron is effectively external, arising between the two outer malpighian tubules. In a more advanced *Eremotermes* species,

E. indicatus, it appears on the inside of a gut loop, but it is the one further forward, the proctodeum having elongated to a greater extent and pushed the very short mesenteron back. The mesenteric extension remains on the same side of the gut, and in *E. nanus* the mixed segment is of typical *Amitermes* form. In *Synhamitermes* the proctodeal overlap appears to have elongated more than that of the mesenteron, and has twisted across the latter. They remain morphologically on the same side as in less developed forms. These elongated mixed segments suggest that this structure may result more from a need to extend the proctodeum than the mesenteron.

Thus within the Amitermitinae as hitherto recognized there are two morphologically quite distinct lines. A parallel development of the mixed segment has taken place on opposite sides of the gut, and there is a radically different attachment of the malpighian tubules. It is therefore relevant to enquire whether the two lines resemble other subfamilies of Termitidae more than each other. In the Termitinae the pattern of the gut is essentially the same as in the second type of Amitermitinae. Minor modifications are found but they appear to be relatively small divergences from the same basic stock. The similarity of the most primitive forms of the first group of Amitermitinae to the Apicotermitinae has already been indicated, and it has been pointed out that numerous intermediates between them and the more specialized forms with a long mixed segment exist. The subfamily Apicotermitinae as conceived by Grassé & Noirot (1954) has not achieved general recognition up to the present time. This is understandable in view of the small number of genera involved, and the fact that the significance of the gut characters had not been fully worked out. Sufficient evidence has now accumulated to provide a new basis for subfamily classification within the Termitidae. These divisions will reflect more clearly the phylogeny of the group and at the same time incorporate the existing knowledge of other characters more satisfactorily. It is proposed to divide the heterogeneous group hitherto named the Amitermitinae between the Apicotermitinae and the Termitinae, as outlined above. The amalgamation of the second group of Amitermitinae with the Termitinae results in the former name becoming a junior synonym since this group includes the type-genus *Amitermes*. This action was suggested by Noirot (personal communication); having considered the alternative of retaining the five subfamilies, and examined many representatives of all of them I now believe he is right, and here give formal expression to his idea. It may be noted that Ahmad (1950) admitted to doubts of the subfamily status of Amitermitinae. He based the only distinction between them and the Termitinae on the length of the apical teeth of the mandibles. This does not bear comparison with much greater differences within other subfamilies, nor does it hold when further species are examined within the groups as he defined them.

The Nasutitermitinae will be retained as a valid subfamily, although their intestinal morphology is clearly derived from the same stock as the Termitinae. The Macrotermitinae with their short intestine like the more primitive families, and four evenly spaced malpighian tubules at the junction of mesenteron and proctodeum, are distinct from the other three subfamilies. Thus the Termitidae will, with the removal of the Amitermitinae, be divided into four subfamilies as shown in Text-fig. 24. The subfamily Apicotermitinae as now constituted will contain 36



- | | | |
|-----------------|------------------|-------------------|
| 1 ACIDNOTERMES | 6 ALYSCOTERMES | 12 ANAOROTERMES |
| 2 AMALOTERMES | 7 AGANOTERMES | 13 ASAGAROTERMES |
| 3 ASTALOTERMES | 8 ACHOLOTERMES | 14 ANENTEOTERMES |
| 4 ADYNATOTERMES | 9 AMICOTERMES | 15 ADERITOTERMES |
| 5 ASTRATOTERMES | 10 APAGOTERMES | 16 ADAIPHROTERMES |
| | 11 ATEUCHOTERMES | |

FIGS 18-23. 18, numbering of enteric valve cushion positions that vary independently; 19, asymmetry of enteric valve resulting from development of positions 3 & 4; 20, asymmetry due to development of position 1; 21-23, comparison of dendrograms of phenetic relationships between genera based on single linkage clustering (21) and median sorting (22) with a hypothetical phylogeny based on conventional criteria (23).

described genera, and several others now known to be awaiting description. They fall readily into two main branches, the more primitive members of which resemble one another in many features, the more specialized diverging considerably in both morphology and behaviour. The formal subfamily diagnosis is followed by a list of the included genera arranged in these two branches and approximately in their hypothetical order of morphological specialization although relationships are distorted by the linear arrangement.

Subfamily APICOTERMITINAE Grassé and Noirot

Apicotermitinae Grassé and Noirot, 1954 : 346-388. Type-genus: *Apicotermes* Holmgren, 1912.

Imago. Labrum at least as broad as long, without transverse sclerotized band, tip partly hyaline; mandibles, apical teeth short or longer than first marginal, left third marginal always separated from second by a distinct notch or indentation; fontanelle variable, oval or round to obsolete, never slit-like.

Soldier. Labrum flap-like, not bifurcate or emarginate in front; mandibles fully developed with one or more marginal teeth. This caste absent in some genera.

Worker. Mandibles similar to imago but with apical and marginal teeth and molar plates more prominent.

General characters. Tibial spurs 3 : 2 : 2 or 2 : 2 : 2. Proventriculus without sclerotized armature; malpighian tubules two (*Labidotermes* only) or four, attached separately to epithelium of mesenteron some distance from its junction with the proctodeum; this junction simple, transverse, or overlapping, with mesenteron extended on inner side of curve of intestine, adjacent to insertion of malpighian tubules, and sometimes dilated at posterior end; first segment of proctodeum tubular, never sac-like, sometimes somewhat inflated; enteric valve unarmed or armed with various sclerotized spiny structures, sometimes invaginated into second proctodeal segment or connected to it by a tubular neck which may bear lobes or diverticula at its anterior end.

The two branches of this subfamily are named after the most widely known genus in each.

'*Apicotermes*-branch'

Labidotermes *Heimitermes*

Eburnitermes *Coxotermes*

Trichotermes *Hoplognathotermes*

Jugositermes *Allognathotermes*

Rostrotermes *Duplidentitermes*

Apicotermes *Acutidentitermes*

Acidnotermes

Amalotermes

Astalotermes

Adynatotermes

Astratotermes

Alyscotermes

'*Anoplotermes*-branch'

Aganotermes

Acholotermes

Amicotermes

Apagotermes

Ateuchotermes

Anaorotermes

Asagarotermes

Anenteotermes

Aderitotermes

Anoplotermes

Adaiphrotermes

Eurytermes

Euhamitermes

Speculitermes

Doonitermes

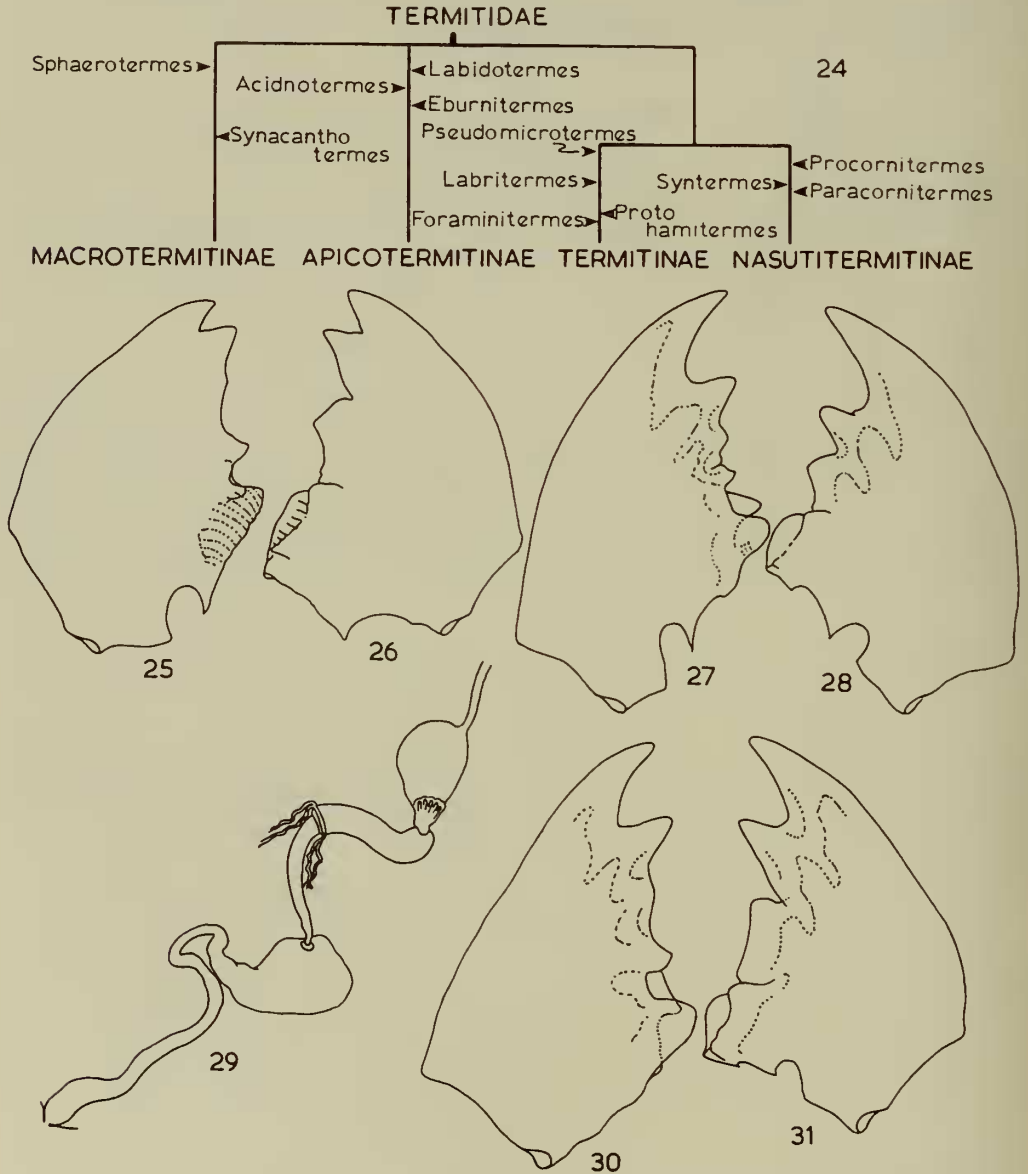
Indotermes

Firmitermes

The '*Anoplotermes*-branch' probably includes several different lines. The relationships between the Ethiopian, Neotropical, and Oriental genera need clarification, which will not be attained until the two latter regions are better known. Some of the longest mixed segments are found in species from the Oriental region, yet here the enteric valve appears to be uniformly unarmed. In the Neotropical region some species lack armature in this structure whilst heavily armed sclerotized valves are found in others. In the Ethiopian region the most elaborate armature occurs in forms showing little or no mesenteric overlap with the proctodeum, but parallel structures with almost as great complexity have developed in lines with a moderately long mixed segment.

The systematic order in which this paper is arranged is based on a subjective assessment of increasing specialization away from the assumed primitive forms.

No other particular relationship of the genera is intended to be implied by their linear succession. Having decided upon the species-membership of the genera, it is possible by applying the single linkage criterion to derive generic dendrograms from the phenograms based on single linkage clustering or median sorting of the



FIGS 24-31. 24, subdivision of Termitidae into four subfamilies, showing hypothetical positions of some of the more primitive genera in each; 25 & 26, *Labritermes*, mandibles of imago; 27 & 28, *Foraminitermes* ditto; 29, 30 & 31, *Pseudomicrotermes*, intestine of worker caste and mandibles of imago.

similarity matrix. These are compared in Text-figs 21, 22 & 23, with a hypothetical dendrogram based on conventional criteria. The generic phenograms are self-explanatory, the distances on the horizontal axes representing percentage similarities as in the specific diagrams, although the actual figures are omitted. The hypothetical phylogeny is drawn with the junctions equally spaced to represent closer or more distant relationships without attempting to quantify them further. Its main difference from the phenograms is the separation of two types of enteric valve specialization. The first and most frequent tends to develop cushion positions (see Text-fig. 18) 3 and 4 more than 1 and 2 as in Text-fig. 19, and progressing beyond this stage to eversion through the valve opening. The other type has the cushions all equally developed or position 1 extended as in Text-fig. 20. Many of the relationships between genera are discussed in more detail under the generic headings in later sections.

Before leaving the subject of phylogeny and the subfamily classification finally it is necessary to specify the fate of the rest of the Amitermitinae, to avoid leaving certain difficult genera ambiguously placed. Apart from the list already given, all other genera present classified in that subfamily become part of the Termitinae, including *Protohamitermes*, *Hoplotermes* and *Labritermes* which have been regarded as among the 'primitive Amitermitinae'. *Protohamitermes* has been discussed earlier. *Hoplotermes* has a gut pattern virtually identical with *Amitermes* but has adapted to soil-feeding. *Labritermes* is a curious genus that shares with *Foraminitermes* a gut layout resembling some of the Termitinae only in having a dilated first proctodeal segment. The malpighian tubules are attached separately to the simple junction of mesenteron and proctodeum. They are evenly spaced and reflexed forwards on the midgut for a short distance before turning back towards the hind gut in a similar manner to some Macrotermitinae. The soldiers of these two genera have similar mandibles and both also have a hyaline tip to the labrum. In the worker and imago castes the proportions of the mandibular teeth differ, *Foraminitermes* having become adapted to soil-feeding by the elongation of apical teeth and loss of molar ridges. In fresh unworn condition both genera retain the second marginal tooth of the left mandible, while that of the right mandible is in the primitive condition with convex anterior and concave posterior edges. Their mandibles are illustrated in Text-figs 25 & 26, 27 & 28. They must be regarded as among the most primitive members of the Termitinae, that not unexpectedly have features in common with similarly placed members of other subfamilies.

One further genus appears to be related to *Labritermes* and *Foraminitermes* in many respects. The soldier of *Pseudomicrotermes* has similar mandibles and a hyaline tip to the labrum. The fontanelle is open and grooves lead forward from it to the base of the labrum. The imago closely resembles that of *Foraminitermes* in colouring, pilosity, the small open fontanelle raised on a minute projection, and the saddle-shaped pronotum. The tibial spurs number 3 : 2 : 2. The proportions of the apical teeth of imago and worker mandibles are intermediate between the two former genera. In fresh unworn specimens of the imago, the second and third marginal teeth of the left mandible are similarly developed to those of *Labritermes*. The second marginal of the right mandible has the straight-edged cutting form seen

in many higher Termitinae of wood- or herbage-feeding lines, but the molar plate lacks ridges like that of *Foraminitermes*. The most distinctive feature of *Pseudomicrotermes* is the intestine. The first segment of the proctodeum is short, ending in a muscular unarmed enteric valve like that of *Foraminitermes*. The malpighian tubules are inserted as bilaterally opposed pairs at the simple transverse mesenteric-proctodeal junction. The gizzard has well-developed typical armature. Thus the gut has many features in common with more primitive groups and the Macrotermitinae, as do the external characters. Its general similarity to *Foraminitermes* apart from the gut, and the paired malpighian tubules suggest that the only position in which *Pseudomicrotermes* can be classified is as an extremely primitive offshoot near the base of the Termitinae. The intestine of this genus is shown in Text-fig. 29 and the imago mandibles in Text-figs 30 & 31.

KEYS TO GENERA

Before attempting to use the keys it will save time if the specimen to be identified is first measured and a set of ratios is worked out. This can be done with a slide-rule in a few minutes. The keys cannot be worked without the ratios which are essential for discrimination between both genera and species. The measurements that are required are given in the list of characters used for the multivariate analyses under the heading (i) *Continuous variables* (p. 12). The characters concerned are numbers 35-59 inclusive. The fixed points for the more novel measurements are illustrated in Text-figs 1, 2 & 3. It is important that the measurements be taken in millimetres and expressed as decimal fractions, as in the tables given under species-descriptions. If other units are used they will affect the scale of complex ratios with different numbers of terms in numerator and denominator, resulting in gross errors. One measurement is best left until actually needed, namely the greatest diameter of the compound eye. This is normally completely size-correlated and of no value. The only exceptions are found in the monotypic *Amicotermes* and two species of *Ateuchotermes*. The ratios required are as follows:

Imago and worker

1. L_A/L_1 (left mandible index)
2. R_A/R_1 (right mandible index)
3. $L_A/L_1.L_m$ (ratio 1 divided by L_m , distance from third marginal to molar notch)
4. Pcl/W (postclypeus length divided by head width)

Imago alone

5. $L_A.R_A/L_1.L_m$ (ratio 3 multiplied by R_A)
6. $R_1/R_A.R_m$ (note difference from ratio 3 for left mandible)
7. Pcl/R_A (postclypeus length divided by right apical to first marginal)
8. M/W (mesonotum width at constriction divided by head width)
9. $L_1/M.N$ (left first to third marginal divided by product of meso- and meta-notal widths)

10. M/R_A (mesonotal width divided by right apical to first marginal)
 11. $O_w/O-E$ (ocellus least diameter divided by ocellus to eye distance)

Worker alone

12. $R_A/R_1.R_m$ (ratio 2 divided by right second marginal to molar notch)
 13. Pcl/R_1 (postclypeus length divided by right first to second marginal)
 14. T_1/T_w (Fore tibia, length divided by greatest width)
 15. $L_m/T_w.L_A$ (complex ratio of tibial width and left mandible measurements)

Imagos

- 1 Left mandible with proximal end of subsidiary marginal tooth hidden behind molar prominence when viewed from the front (Text-fig. 45). Head capsule very glossy, pilosity of sparse fine setae forming a pelt with regularly spaced paired emergent setae among them. Fore tibia with three apical spurs, third vestigial and difficult to detect. Fontanelle conspicuous elongate-oval, larger than ocellus. Small to medium-sized, $W, 0.81-0.90$ **AMALOTERMES** (p. 47)
- Left mandible with proximal end of subsidiary marginal tooth at least level with edge of molar prominence, clear of it in most genera, when viewed from the front. Head capsule not markedly glossy, pilosity, when it forms a pelt, with scattered, not regular emergent setae. Fore tibia with two or three definite apical spurs, third rarely vestigial. Fontanelle seldom larger than ocellus, if so, either more than twice as large, or entire specimen larger, $W, 1.03-1.20$ 2
- 2 Fore tibia with only two apical spurs, no trace of third, outer spur **ADAIPHROTREMES** (p. 229)
- Fore tibia with three apical spurs, third usually distinct though smaller than inner pair, only vestigial in three widely unrelated species 3
- 3 Left mandible with proximal end of subsidiary marginal tooth level with edge of molar prominence, viewed from the front 4
- Left mandible with proximal end of subsidiary marginal tooth clear of edge of molar prominence, viewed from the front 8
- 4 Small, $W, 0.57-0.66$ **ACIDNOTERMES** (p. 44)
- Larger, $W, 0.99-1.21$ 5
- 5 Apical teeth of mandibles shorter, $L_A/L_1, 0.51-0.57, R_A/R_1, 0.73-0.87$ 6
- Apical teeth of mandibles longer, $L_A/L_1, 0.79-1.04, R_A/R_1, 1.11-1.45$ 7
- 6 Larger, $W, 1.14-1.21$. Ocelli separated from compound eyes by two-fifths own least diameter or more. Postclypeus moderately inflated, $Pcl/W, 0.27-0.31$. Meso- and metanota rather narrow at constriction, $M/W, 0.24-0.28$, complex ratio $L_1/M.N, 1.76-2.32$. Pilosity of head uneven, not forming a pelt **ADYNATOTERMES** (p. 102)
- Smaller, $W, 0.98-1.04$. Ocelli very large, almost touching compound eyes or separated by up to one-quarter own least diameter. Postclypeus weakly inflated, $Pcl/W, 0.23$. Meso- and metanotum wider at constriction, $M/W, 0.29-0.33$, complex ratio $L_1/M.N, 0.54-0.56$. Pilosity of head an even pelt with emergent setae **ATEUCHOTERMES** (p. 158)
- 7 Meso- and metanota wider at constriction, $M, 0.31, N, 0.33-0.35, M/W, 0.30-0.32$ **ACHOLOTERMES** (p. 139)
- Meso- and metanota narrower at constriction, $M, 0.24-0.28, N, 0.22-0.27, M/W, 0.21-0.24$ **AGANOTERMES** (p. 135)
- 8 Meso- and metanota proportionately narrower at constriction, M/W under 0.26, or if more, complex ratio $L_1/M.N$ over 2.4. Compound eyes not prominent, somewhat flattened, back of head narrowly rounded behind them. Smaller, $W, 0.69-1.10$, only two species over 0.98 9

- Meso- and metanota proportionately wider at constriction, M/W over 0.26, or if less, $L_1/M.N$ under 2.4. Compound eyes prominent in proportion to own diameter, back of head more widely rounded. Mostly larger, W, 0.76-1.33, only three species under 0.98 (only one entire range less) 11
- 9 Apical teeth of mandibles longer, L_A/L_1 , 0.78-0.80, R_A/R_1 , 1.09-1.18; larger, W, 1.03-1.10 (better separation from other half-couplet given by complex ratios $L_A.R_A/L_1.L_m$, 1.45-1.60; $R_1/R_A.R_m$, 11.5-12.4, but also note size difference) **ASAGAROTERMES** (p. 187)
- Apical teeth of mandibles shorter, L_A/L_1 , 0.42-0.79, R_A/R_1 , 0.62-1.05; smaller, W, 0.65-1.06, those with longer apical teeth, small, W less than 0.85 (complex ratios $L_A.R_A/L_1.L_m$, 0.46-1.37; $R_1/R_A.R_m$, 16.2-31.6 10
- 10 Postclypeus weakly inflated, without well defined median suture or posterior margin, Pcl/W , 0.20-0.22; small, W, 0.74 **APAGOTERMES** (p. 155)
- Postclypeus usually more strongly inflated with median suture and distinct posterior margin, Pcl/W , 0.21-0.36; those species in which not so, larger, W over 0.85 **ASTALOTERMES** (Group I) (p. 51)
ANENTEOTERMES (p. 192)
- 11 Apical teeth of mandibles longer, L_A/L_1 , 0.68-1.04, complex ratio $L_A/L_1.L_m$, 11.59-16.29. Pilosity of head capsule dense, uneven, not forming a pelt. Fontanelle inconspicuous in species or genera with shortest apical teeth 12
- Apical teeth of mandibles mostly shorter, L_A/L_1 , 0.41-0.80 (only two spp. over 0.68, not all specimens of one of these), complex ratio $L_A/L_1.L_m$, 4.54-11.11 (only one sp. over 10.60). In species with mandible characters overlapping with first half-couplet, pilosity of head capsule rather sparse, fine and even, forming a pelt with scattered emergent setae, and fontanelle large or pale and conspicuous 13
- 12 Compound eyes relatively small, W/E , 4.5, head capsule nearly semi-circular behind them **AMICOTERMES** (p. 152)
- Compound eyes normal sized, W/E , under 4.0, head capsule distinctly less than semi-circular behind them **ACHOLOTERMES** (p. 139)
- 13 Fontanelle shape generally regularly oval to long oval **ASTALOTERMES** (Groups II & III) (p. 51)
ALYSCOTERMES (p. 125)
ASTRATOTERMES (p. 105)
- Fontanelle circular or irregular, may be broader than long, outline sometimes indistinct 14
- 14 Pilosity of head capsule short and even, forming a pelt with longer emergent setae 15
- Pilosity of head uneven, not forming a pelt 17
- 15 Fontanelle circular, sharply defined, much paler in colour than head capsule and contrasting with it 16
- Fontanelle irregularly circular or short oval, not sharply defined, paler than head but not contrasting **ATEUCHOTERMES** (p. 158)
- 16 Ocellus separated from compound eye by less than own least diameter, $O_w/O-E$, 1.14-2.05. Apical tooth of left mandible shorter, L_A/L_1 , 0.54-0.68 **ADERITOTERMES** (p. 222)
- Ocellus separated from compound eye by approximately own least diameter, $O_w/O-E$, 0.96-1.07. Apical tooth of left mandible longer, L_A/L_1 , 0.68-0.78 **ASTRATOTERMES** (p. 105)
- 17 Fontanelle circular, pale, only slightly smaller than ocellus. Postclypeus with evenly rounded posterior margin **ASTRATOTERMES** (p. 105)
- Fontanelle irregular, nearly triangular, less than half size of ocellus. Postclypeus with posterior margin rounded in middle, straighter towards outer corners **ANAOROTERMES** (p. 184)

Workers

- 1 Mixed segment of gut long, anterior termination of proctodeal overlap distinctly to left side of malpighian knot in ventral view (Text-figs 520-532, 585-603, 621-627 & 648-658) 2
- Mixed segment of gut short, anterior end of proctodeal overlap on right side of malpighian knot or at most within it in ventral view, or junction between mesenteron and proctodeum transverse, without overlap, mixed segment absent 4
- 2 Mesenteron with spherical or hemispherical dilation at posterior end of mixed segment. Fore tibia moderately to strongly inflated, T_1/T_w , 3.08-4.00, with only two apical spurs. Enteric valve without armature, surface of cushions reticulated, sometimes scaly at anterior ends **ADAIPHROTERMES** (p. 229)
- Mesenteron not distinctly dilated at posterior end of mixed segment. Fore tibia not or moderately inflated, T_1/T_w , 3.58-5.31, with three apical spurs. Enteric valve cushions with scaly surface, or armed with spines or spicules, sometimes protruding through valve opening at posterior ends (Plates 7, 8 & 9, excl. figs 10-12) 3
- 3 Enteric valve seating fully mid-dorsal in position in unopened abdomen (Text-fig. 6) with three equal and conspicuous lobes. Cushions of valve all equally developed, thickly armed at posterior ends with elongated spicules or protruding through valve opening as transparent flattened vanes. Larger, W, 0.90-1.00; complex ratio $L_m/T_w.L_A$, 3.23-4.83 **ADERITOTERMES** (p. 222)
- Enteric valve seating lateral or dorso-lateral in position in unopened abdomen, with two or three weak lobes. Cushions of valve not equally developed, positions 3 and 4 larger, sometimes protruding through valve opening, armature when present spiny, not spicules. Smaller, W, 0.56-0.84; complex ratio $L_m/T_w.L_A$, 5.01-7.85 **ANENTEOTERMES** (p. 192)
- 4 Enteric valve cushions armed posteriorly with conspicuous spines or spicules protruding through valve opening 5
- Enteric valve cushions unarmed posteriorly, or with minute spines or spicules not protruding through valve opening 10
- 5 Armature of enteric valve more or less radially symmetrical with all cushions nearly equally developed 6
- Armature of enteric valve asymmetrical with one or two cushion positions much more developed than the rest 8
- 6 Head capsule brown. Left mandible with proximal end of subsidiary marginal tooth hidden behind molar prominence in surface view. Third spur of fore tibia vestigial. Overlap between mesenteron and proctodeum diagonal. Armature of enteric valve of short stout spines on posterior ends of cushions only (Pl. 1) **AMALOTERMES** (p. 47)
- Head capsule yellow. Left mandible with proximal end of subsidiary marginal tooth not hidden behind molar prominence. Third spur of fore tibia distinct. Junction between mesenteron and proctodeum nearly transverse, no appreciable overlap. Armature of enteric valve of long thin spines or spicules extending from about half length of cushions to distal ends 7
- 7 Smaller, W, 0.58. Apical teeth of mandibles shorter, L_A/L_1 , 0.52. Postclypeus less inflated, Pcl/R_1 , 1.80. Enteric valve seating with very short neck, weakly 2- or 3-lobed. Armature of enteric valve arranged in rather regular transverse rows, subsidiary spines below distal fringe slightly spatulate at tips (Pl. 4) **APAGOTERMES** (p. 155)
- Larger, W, 0.76. Apical teeth of mandibles longer, L_A/L_1 , 1.09. Postclypeus more inflated, Pcl/R_1 , 3.28. Enteric valve seating with very long neck, definitely 3-lobed. Armature of enteric valve not regularly arranged, all spines thin and evenly tapered (Pl. 3) **AMICOTERMES** (p. 152)

- 8 Enteric valve cushions in positions 3 and 4, and their armature, much more strongly developed than positions 1 and 2 (Text-fig. 19) 9
 - Enteric valve cushion in position 1 elongated and its armature more strongly developed than positions 2 3 and 4, which are subequal (Text-fig. 20)
A TEUCHOTERMES (p. 158)
- 9 Enteric valve cushions in position 3 everted, hemispherical, and armed with stout spines; position 4 fork-like, with 7-8 curved tines; other positions reduced, two with 1-2 spines, one absent (Pl. 7) **ANAOROTERMES** (p. 184)
 - Enteric valve cushions in positions 3 and 4 fringed with stout spines other positions smaller with few spines or none (Pl. 2) **ALYSCOTERMES** (p. 125)
- 10 Left mandible with proximal end of subsidiary marginal tooth hidden behind molar prominence in surface view. Very small, W, 0.48-0.57 **ACIDNOTERMES** (p. 44)
 - Left mandible with proximal end of subsidiary marginal tooth clear of molar prominence in surface view. Larger, W, 0.58-1.09 11
- 11 Enteric valve armature consisting of sclerotized spiked coronet-like bands, one girdling the middle of each cushion, all equally developed (Pl. 7)
ASAGAROTERMES (p. 187)
 - Enteric valve armature not so 12
- 12 Enteric valve unarmed, cushions with reticulate or scaly surface, single exception smaller, W, 0.64-0.69 13
 - Enteric valve armature, edges of scales on cushion surface each produced into one or more small spines or spicules, generally larger, W, 0.70-1.09. 15
- 13 Apical teeth of mandibles very long, L_A/L_1 , 0.97-1.00, R_A/R_1 , 1.25-1.29; complex ratio $L_A/L_1.L_m$, 25.81-26.66 **AGANOTERMES** (p. 135)
 - Apical teeth of mandibles shorter, L_A/L_1 , 0.43-0.86, R_A/R_1 , 0.57-1.08; complex ratio $L_A/L_1.L_m$, 7.25-18.60 14
- 14 Enteric valve seating ventral on left side of unopened abdomen, with two prominent bilaterally opposed erect lobes (virtually diverticula) **ADYNATOTERMES** (p. 102)
 - Enteric valve seating ventro- to dorso-lateral, weakly to prominently 2- or 3-lobed but never with erect opposed diverticula **ASTALOTERMES** (p. 51)
- 15 Apical teeth of mandibles longer, complex ratios $L_A/L_1.L_m$, 20.75-22.89, $R_A/R_1.R_m$, 22.80-30.15. Postclypeus more inflated, Pcl/R_1 , 2.57-2.88
ACHOLOTERMES (p. 139)
 - Apical teeth of mandibles shorter, complex ratios $L_A/L_1.L_m$, 7.47-18.61, $R_A/R_1.R_m$, 8.86-21.90. Postclypeus less inflated, Pcl/R_1 , 1.65-2.60, only one specimen recorded over 2.4 **ASTRATOTERMES** (p. 105)

ACIDNOTERMES gen. n.

(Akidnos, Gr., 'Weak, feeble')

Type-species: *Acidnotermes praus* sp. n.

Imago. Very small, W, 0.57-0.66. Fore tibia with three apical spurs, third well developed, two-thirds length of other two. Apical teeth of mandibles short, L_A/L_1 , 0.50-0.56, R_A/R_1 , 0.62-0.71; subsidiary marginal tooth of left mandible with proximal end just level with edge of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 10.00-14.41. Right mandible with points of apical and marginal teeth in line, but second marginal wide with anterior edge longer than that of first marginal. Meso- and metanota narrow at constriction, M/W , 0.21, transverse dark sutures weak but present.

Worker. Very small, W, 0.48-0.57. Fore tibia moderately swollen, T_1/T_w , 3.46-3.94, with three apical spurs, third nearly as large as other two. Apical teeth of mandibles short, L_A/L_1 , 0.48-0.54, R_A/R_1 , 0.60-0.68; subsidiary marginal tooth of left mandible with proximal end hidden behind molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 11.55-14.72.

Right mandible similarly proportioned to that of imago except for enlarged molar plate, complex ratio $R_A/R_1.R_m$, 13.40–18.15. Mesenteric junction with proctodeum simple, nearly transverse, without overlap, mesenteron short with malpighian tubules inserted at exactly half its length. First section of proctodeum slightly longer than mesenteron, slightly swollen, tapering distally to enteric valve; valve seating a simple rim, sessile on second pouch of proctodeum, latero-ventral in position in unopened abdomen; internal cushions of enteric valve, unarmed, weakly scaled.

This genus, represented so far by a single species, is clearly related to *Astalotermes*, and particularly to *A. comis* sp. n. However, the position of the subsidiary marginal tooth of the left mandible, and the distinctly shorter gut of the worker, are both features resembling more primitive groups. The results of the various numerical taxonomic analyses also separate *Acidnotermes* to such an extent that it must be placed in a different genus. Its small size and mandible form combined distinguish it from all other genera. The only overlap in size is found in *Anenteotermes nanus* (Sjöstedt) but here the mandibles are distinctive in both castes, and the worker with its long mixed segment of the gut, and armed enteric valve, presents no problems.

The relative shortness of the worker gut, the lack of a mixed segment, the unarmed enteric valve, and the unspecialized mandibles, all lead to the opinion that *Acidno-*



FIGS 32–42. *Acidnotermes praus*. 32, 33, front and side views of imago head capsule; 34, 35, imago mandibles; 36–38, worker ditto; 39, entire worker intestine; 40, mesenteric-proctodeal junction showing attachment of malpighian tubules and position of malpighian knot; 41, 42, views of enteric valve seating.

termes probably closely resembles the ancestral forms of the group. This is why *Acidnotermes* is placed first in the systematic order of arrangement of this paper. The only external characters of worker or imago that I would regard as likely to be specialized are the swollen fore tibia of the former and the narrow meso- and metanota of the latter. The insertion of the malpighian tubules at the mid-point of the mesenteron instead of nearer to the junction with the proctodeum probably also represents a specialization carried a little further in this genus than in any other.

Acidnotermes praus sp. n.

(Text-figs 32-42; Pl. I, fig. 1)

Imago. Head capsule brown, sepia-brown above ocelli, dark areas sometimes extending as tapering streaks converging to fontanelle; fontanelle minute, circular to elongate oval, slightly raised on small bump, pale yellow-brown; medial spot circular or short oval, smaller than fontanelle, also raised on small bump, brown; postclypeus pale brown, labrum pale yellow; frontal marks very indistinct pale brown; antennae pale yellow-brown. Pronotum, meso- and metanota pale brown; legs, femora and tibiae pale yellow-brown, tarsi pale yellow. Abdominal tergites pale yellow-brown, dorsal stigmata paler, yellow; sternites, very pale yellow-brown laterally, yellow-white in middle, ventral stigmata darker, pale yellow-brown, cerci yellow-white.

Posterior margin of head capsule evenly rounded except immediately behind compound eyes, ocelli proportionately rather large, separated from eyes by less than half own least diameter, nearly touching in some specimens; postclypeus moderately inflated, Pcl/W, 0.25-0.30 posterior margin rounded, somewhat more arched in middle, median suture distinct. Pilosity of head capsule very dense, pale, slightly uneven in length, scarcely forming a pelt.

Measurements (10 specimens from five localities) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	0.57-0.66	0.596 \pm 0.030
Ocellus ($O_w \times O_l$) . . .	0.05-0.06 \times 0.07-0.09	0.058 \pm 0.004 \times 0.077 \pm 0.006
Ocellus to eye (O-E) . . .	0.01-0.02	0.014 \pm 0.005
Postclypeus length (Pcl) . . .	0.15-0.18	0.160 \pm 0.009
Antennal article III . . .	0.01-0.02	0.015 \pm 0.003
Antennal article IV . . .	—	0.022 \pm 0.002
Antennal article V . . .	0.02-0.03	0.023 \pm 0.002
Left mandible, apical to first marginal (L_A) . . .	0.04-0.05	0.045 \pm 0.002
Left mandible, first to third marginal (L_1) . . .	0.08-0.09	0.085 \pm 0.004
Left mandible, third marginal to molar (L_m) . . .	0.04-0.05	0.045 \pm 0.003
Right mandible, apical to first marginal (R_A) . . .	0.04-0.05	0.047 \pm 0.002
Right mandible, first to second marginal (R_1) . . .	0.06-0.08	0.071 \pm 0.005
Right mandible, second marginal to molar (R_m) . . .	0.04-0.05	0.046 \pm 0.003
Mesonotum width (M) . . .	0.10-0.15	0.128 \pm 0.002
Metanotum width (N) . . .	0.10-0.14	0.121 \pm 0.002

Worker. Head capsule pale yellow, pilosity yellow, fairly numerous but very short. Postclypeus strongly inflated, Pcl/W, 0.33–0.36, Pcl/R₁, 2.83–3.19. Membranous wall of enteric valve beyond cushions with sparse minute spicules. Other characters given in generic diagnosis.

Measurements (five specimens from five localities) in millimetres.

	Range	Mean ± S.D.
Head width (W)	0.48–0.57	0.519 ± 0.032
Fore tibia width (T _w)	—	0.099 ± 0.001
Fore tibia length (T _l)	0.34–0.39	0.358 ± 0.021
Postclypeus length (Pcl)	0.17–0.19	0.182 ± 0.009
Left mandible, apical to first marginal (L _A)	—	0.039 ± 0.002
Left mandible, first to third marginal (L ₁)	0.07–0.08	0.076 ± 0.004
Left mandible, third marginal to molar (L _m)	—	0.038 ± 0.002
Right mandible, apical to first marginal (R _A)	—	0.039 ± 0.002
Right mandible, first to second marginal (R ₁)	0.06–0.07	0.061 ± 0.004
Right mandible, second marginal to molar (R _m)	0.04–0.05	0.039 ± 0.004

The distinguishing features of this species are discussed under the generic heading, and some details of its phylogenetic significance are mentioned in the section on the phylogeny of the group as a whole. The abdomen of the worker caste appears to be dehiscant in at least some specimens but this characteristic does not seem to be as strongly developed as in some species of *Astalotermes*.

Holotype ♀ imago, paratype ♂ and ♀ imagos, and workers from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Stanleyville, 27.v.1948 (*A. Emerson*), in American Museum of Natural History.

Other paratype material. DEMOCRATIC REPUBLIC OF CONGO: Luluabourg, xi.1929 (*J. Ghesquière*); Camp Putnam, Epulu R., 20.v.1948, Stanleyville, 25, 27.v, and 1.vi.1948, five vials, 20 km E. of Ndjili and 18 km S. of Leopoldville [Kinshasa], 10.vi.1948 (*A. Emerson*); Kinshasa, 5.xii.1959, two vials, 25.vi.1960, 1.x.1966, Mpenzara, 7.ix.1966 (*A. Bouillon*); Kinshasa, 13.v.1965, two vials, Mount Gafula, 30 km S. of Kinshasa, on Matadi Road, 4.x.1966 (*C. Nkakala*); Mondongo, Lisala, 27–28.ix.1966, three vials (*J. Ruelle*). Material in AMNH, BMNH and Coll. A. Bouillon, University of Lovanium, Kinshasa.

A total of 20 nest-series were examined.

The species appears to be fairly common in the Congo Forest block, where it has been found in small compact earth-carton nests 10–15 cm in diameter, on or below the soil surface, as well as in the mounds of other species, in surface debris, and under dead wood.

AMALOTERMES gen. n.

(Amalos Gr., 'soft, tender, or weak')

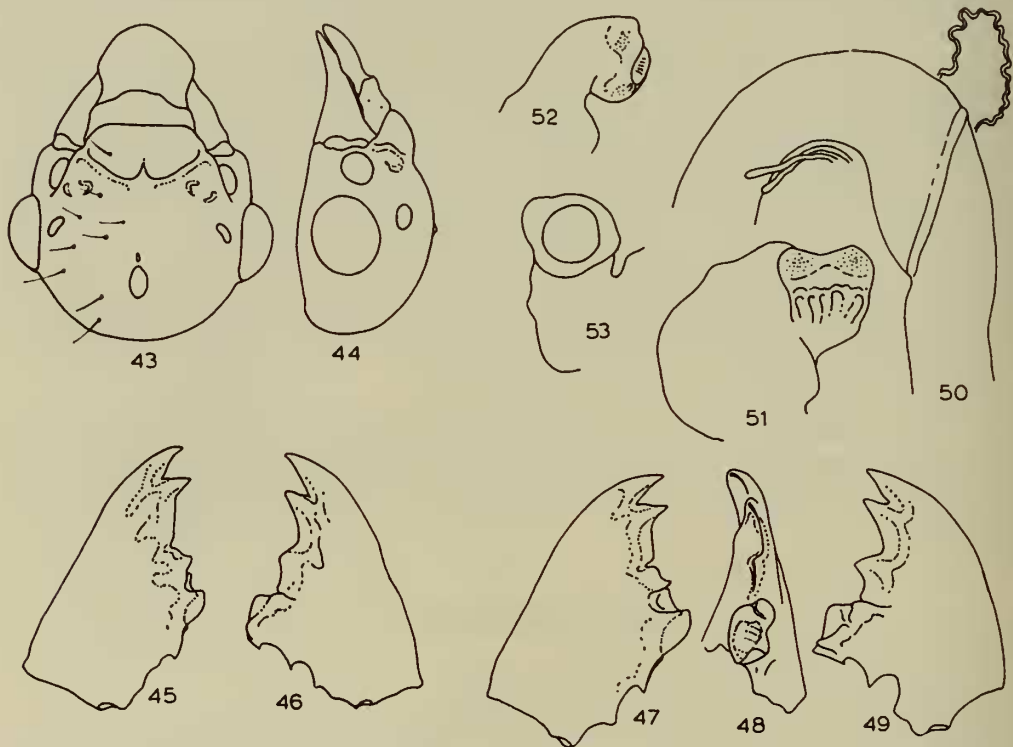
Type-species: *Amalotermes phaeocephalus* sp. n.

Imago. Medium-sized, W, 0.81–0.90. Fore tibia with three apical spurs, but third vestigial, almost lost in some specimens. Apical teeth of mandibles short, L_A/L₁, 0.38–0.48, R_A/R₁, 0.56–0.65; subsidiary marginal tooth of left mandible with proximal end hidden behind molar prominence in surface view, complex ratio L_A/L₁.L_m, 6.50–8.29. Right mandible with anterior edge of first marginal tooth about as long as that of second, its point slightly behind the line of

apical and second marginal teeth. Meso- and metanota fairly wide at constriction, M/W , 0.25–0.28, transverse dark sutures distinct, usually sharp and clear, sometimes more diffuse.

Worker. Medium-sized, W , 0.74–0.79. Fore tibia slender, T_1/T_w , 6.14–6.43, with three apical spurs, but third vestigial, almost lost in most specimens. Apical teeth of mandibles short, L_A/L_1 , 0.41–0.51, R_A/R_1 , 0.53–0.66; subsidiary marginal tooth of left mandible with proximal end hidden behind molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 8.60–9.40. Right mandible with anterior edge of first marginal tooth distinctly shorter than that of second, complex ratio $R_A/R_1.R_m$, 10.59–11.20. Mesenteric overlap at junction with proctodeum about twice as long as width of mesenteron at insertion of malpighian tubules, reaching half way through malpighian knot. Enteric valve seating weakly two-lobed, connected to second pouch of proctodeum by a short neck, lateral in position in unopened abdomen; internal cushions of enteric valve all more or less equally developed and armed distally with prominent stout spines protruding through valve opening.

The single species of *Amalotermes* presents an unusual mosaic of characters, some regarded as primitive, others as specialized, which makes it impossible to fit it into a genus with any other known species. This conclusion, reached by conventional means, is confirmed by its position in the various multivariate analyses. In both single linkage and median clustering methods of examining the similarity matrix it is in the last three species to be grouped, and this isolation is confirmed by the



FIGS 43–53. *Amalotermes phaeocephalus*. 43, 44, front and side views of imago head capsule; 45, 46, imago mandibles; 47–49, worker ditto; 50, mesenteric-proctodeal junction showing attachment of malpighian tubules and position of malpighian knot; 51–53, views of enteric valve seating.

principal co-ordinates, plotted in Text-fig. 12. Its nearest neighbour in these analyses is another isolated species, *Apagotermes stolidus* sp. n. From this it differs in the imago by the proportions and positions of the mandibular teeth, the large and conspicuous fontanelle, the wider meso- and metanota, and the vestigial third spur of the fore tibia. In the worker, the mandible and fore tibia spur characters also apply; moreover, *Amalotermes* has a longer mesenteric overlap with the proctodeum, and very different enteric valve armature from *Apagotermes*. The same characters also serve to distinguish *Amalotermes* from similarly sized members of the other genera such as *Astalotermes* and *Anenteotermes*.

The relationships of *Amalotermes* to other genera are not easy to assess. The mandible form and slender fore tibia of the worker are features common to the more primitive members of the group and the brown head of the worker caste recalls genera such as *Speculitermes*. Its liking for rotting wood also suggests a lack of specialization in habits. However, the reduced alate pilosity and vestigial third tibial spur are derivative characters as are, in the worker, the already more elongated gut and well developed enteric valve armature. It most probably represents a persistent early offshoot from the main group, and has developed its own specialized characters; some of these are convergently resembled by other genera that perhaps diverged from the main stem rather later on.

Amalotermes phaeocephalus sp. n.

(Text-figs 43-53; Pl. I, fig. 2)

Imago. Head capsule very glossy dark sepia-brown, sometimes darker above ocelli; fontanelle larger than ocellus, oval, flat or slightly depressed, pale brown; medial spot minute, oval, slightly raised on small bump, sepia-brown; postclypeus sepia-brown, labrum brown; frontal marks almost obsolete, flat, sepia-brown; antennae, sepia-brown. Pronotum sepia-brown, meso- and metanota brown; legs entirely yellow-white. Abdominal tergites sepia-brown, sternites laterally brown, pale yellow in middle, abdominal stigmata almost absent, coloured as sclerites; cerci very pale brown.

Posterior margin of head capsule evenly rounded, ocelli rather small, separated from compound eyes by three-quarters own least diameter or more; postclypeus not strongly inflated, Pcl/W, 0.21-0.24, posterior margin rounded, more arched in middle, median suture absent or very weakly developed. Pilosity of head capsule rather long, somewhat sparse and fine, brown, forming a very distinct long pelt with regularly placed paired emergent setae.

Measurements (three specimens from three localities) in millimetres.

	Range	Mean
Head width across eyes (W)	0.81-0.90	0.848
Ocellus ($O_w \times O_l$)	0.06-0.07 \times 0.09-0.10	0.063 \times 0.091
Ocellus to eye (O-E)	0.05-0.06	0.056
Postclypeus length (Pcl)	0.18-0.21	0.190
Antennal article III	0.04-0.06	0.048
Antennal article IV	—	0.049
Antennal article V	—	0.050
Left mandible, apical to first marginal (L_A)	0.05-0.06	0.053
Left mandible, first to third marginal (L_1)	0.12-0.13	0.121

Left mandible, third marginal to molar (L _m)	0.05-0.06	0.058
Right mandible, apical to first marginal (R _A)	0.05-0.07	0.060
Right mandible, first to second marginal (R ₁)	0.09-0.10	0.097
Right mandible, second marginal to molar (R _m)	0.05-0.06	0.058
Mesonotum width (M)	0.21-0.25	0.224
Metanotum width (N)	0.20-0.29	0.238

Worker. Head capsule brown, pilosity yellow-brown, fontanelle conspicuous, very pale brown; antennae sepia-brown. Postclypeus not strongly inflated, Pcl/W, 0.22-0.25, Pcl/R₁, 1.86-1.91. Membranous wall of enteric valve beyond cushions with sparse minute spicules. Other characters given in generic diagnosis.

Measurements (three specimens from three localities) in millimetres.

	Range	Mean
Head width (W)	0.74-0.79	0.754
Fore tibia width (T _w)	0.09-0.10	0.091
Fore tibia length (T _l)	0.54-0.63	0.575
Postclypeus length (Pcl)	0.16-0.18	0.175
Left mandible, apical to first marginal (L _A)	0.05-0.06	0.053
Left mandible, first to third marginal (L ₁)	0.11-0.12	0.115
Left mandible, third marginal to molar (L _m)	0.05-0.06	0.051
Right mandible, apical to first marginal (R _A)	0.05-0.06	0.053
Right mandible, first to second marginal (R ₁)	0.09-0.10	0.093
Right mandible, second marginal to molar (R _m)	0.05-0.06	0.053

The comparisons of this species with others are largely made under the generic heading, and its relationships are also discussed. There is little to add except that the abdomen of the worker caste appears to have at least a tendency to dehiscence. One further curious feature is the lack of male imagos in the collections. Long nest-series are available with many de-alated semi-physogastric females and numerous eggs and larvae, but only a single male is known. This is not from one of these long series, which perhaps may provide examples of parthenogenetic colonies, a phenomenon rare in termites.

Holotype ♀ imago, paratype ♀ imagos and workers from type-colony, NIGERIA: Eastern Region, 40 miles from Port Harcourt on Owerri Road, 19.vi.1957 (*W. Wilkinson*, Coll. No. WW747), in British Museum (Natural History).

Other paratype material. NIGERIA: Western Region, Sobo Plain, Obanokoro, 4.iii.1957, Eastern Region, 40 m. and 36 m. from Port Harcourt on Owerri Road, 19.vi.1957, 2 vials, and 5.xii.1957 (*W. Wilkinson*). GABON: Belinga, 13.vi.1962 (*J. Deligue*). DEMOCRATIC REPUBLIC OF CONGO: Camp Putnam, Epulu R., 20.v.1948, and Stanleyville, 27.v.1948 (*A. Emerson*) in AMNH; Kivu, Irangi, 3 and 7.xi.1963 (*E. Ernst*) his own collection.

A total of nine nest-series were examined.

Although not particularly common, this species seems to be widespread in the

equatorial part of the Congo forest. It has been found in the old decaying mounds of other species, and in moist rotting wood, under bark, and similar situations.

ASTALOTERMES gen. n.

(Astales, Gr., 'unarmed')

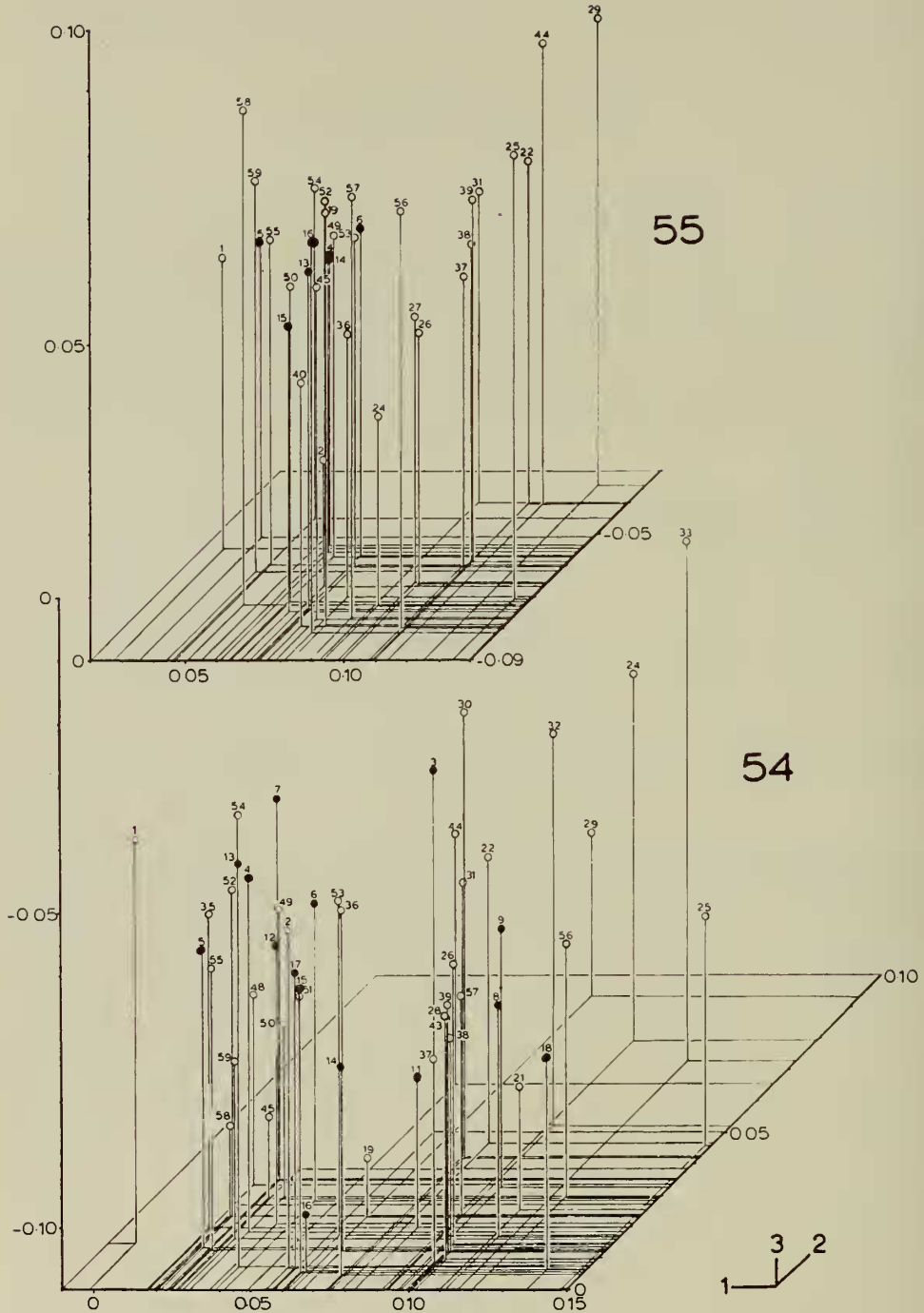
Type-species: *Anoplotermes concilians* Silvestri, 1914 : 58.

Imago. Small to large, W, 0.69-1.33. Fore tibia with three apical spurs, third usually only slightly smaller than other two, sometimes vestigial. Apical teeth of mandibles vary in length from short to fairly long, L_A/L_1 , 0.41-0.79, R_A/R_1 , 0.55-1.05; subsidiary marginal tooth of left mandible with proximal end just clear to distinctly clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 4.54-13.20. Right mandible with points of apical and marginal teeth in line, or first marginal retracted behind line from apical to second marginal; anterior edge of first marginal longer than that of second, equal to it, or shorter. Meso- and metanota from narrow to wide at constriction, M/W, 0.20-0.36, meso- and metanotal sutures present to absent.

Worker. Small to large, W, 0.58-1.08. Fore tibia slender to moderately swollen, T_1/T_w , 3.86-5.96 with three apical spurs, third usually distinct but sometimes vestigial. Apical teeth of mandibles short to fairly long, L_A/L_m , 0.43-0.86, R_A/R_1 , 0.57-1.08; subsidiary marginal tooth of left mandible with proximal end just clear to distinctly clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 7.25-18.60. Right mandible, with points of apical and marginal teeth in line, or first marginal retracted; anterior edge of first marginal slightly longer than that of second, equal to it, or shorter, complex ratio $R_A/R_1.R_m$, 9.94-22.15. Mesenteric junction with proctodeum varies from almost transverse to overlapping by about twice width of mesenteron at insertion of malpighian tubules, proximal end of proctodeum touching malpighian knot. Enteric valve seating variable, weakly lobed and sessile to distinctly two- or three-lobed and connected to second pouch of proctodeum by a definite neck, ventro to dorso-lateral in position in unopened abdomen; internal cushions of enteric valve unarmed, surface scaly.

A genus that occupies a transitional position between others with more primitive and more specialized characters is always difficult to define and *Astalotermes* is no exception to this. The diagnoses given above clearly include so wide a range of variation that they overlap to some extent with several other genera, particularly in the imago caste. It will be noted from the keys to genera that imagos alone are not always reliably identifiable at this level; the worker caste usually gives a clearer set of characters. The short mesenteric overlap with the proctodeum distinguishes it from *Adaiaphrotermes*, *Anenteotermes* and *Aderitotermes*. The unarmed enteric valve separates it from many monotypic genera, from *Alyscotermes* and *Ateuchotermes*, and from its near relative *Astratotermes* in which the scales bear small teeth. *Adynatotermes* is clearly closely related but has a more specialized enteric valve seating; *Aganotermes* and *Acholotermes* have longer apical teeth to the mandibles in both imago and worker castes. The relationship to *Acidnotermes* is indicated under that genus.

The species now placed in *Astalotermes* were grouped differently at earlier stages in this revision. The multivariate analyses of measurements alone—canonical variates (Text-figs 54 & 55) and principal components—produced compact groupings of some of the species, but others now included were scattered more widely or



FIGS 54 & 55. Three-dimensional graphs of canonical variates 1, 2 & 3, showing species of *Astalotermes* as solid spots. 54, imago, 55, worker caste.

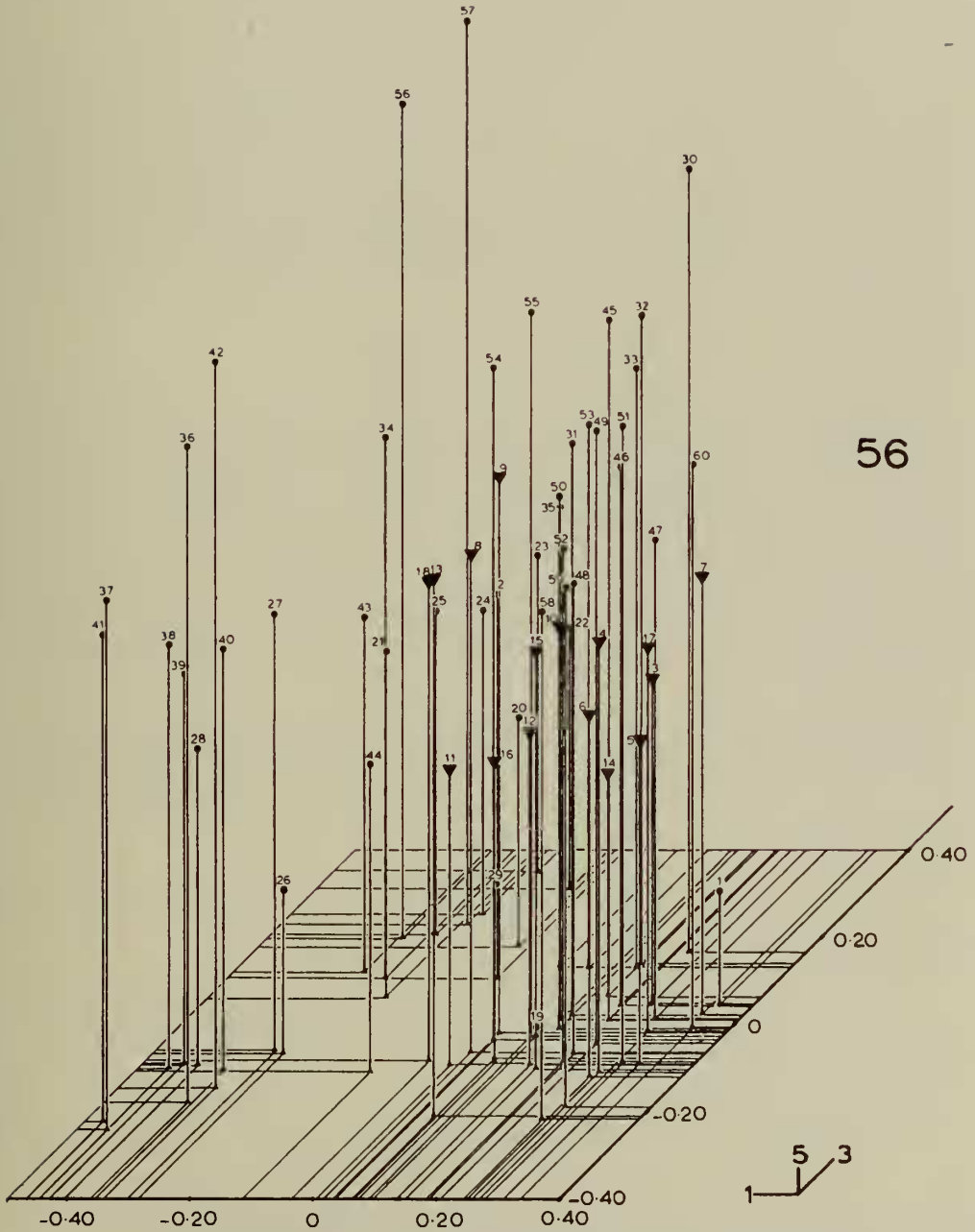


FIG. 56. Three-dimensional graph of principal co-ordinates analysis-plot of eigenvectors 1, 3 & 5 showing species of *Astalotermes* marked by large triangles forming a loose cluster.

grouped at some distance from the rest. Various arrangements were tried in efforts to obtain well-defined genera. These were based in turn on differences in the position and form of the worker enteric valve seating, in the proportions of imago and worker mandibles, and in the widths of imaginal thoracic nota. However, the results of cluster and vector analyses of the similarity matrix placed the species in a single rather large loose cluster, near to the genera *Adaiaphrotermes*, *Acholotermes* and *Anenteotermes* (Text-fig. 56). When the stage of preparing keys to genera was reached it quickly became clear that the groupings previously tried would not key out at all. For practical purposes the grouping indicated by overall similarity was better than any of the others tried earlier, and was therefore adopted. It should be noted that consequent on the heavy weighting imposed on the enteric valve characters by the coding used, the genus is essentially defined by its lack of armature in this feature.

Species-Groupings

Although the earlier attempts at clustering proved to be at too low a level, some of the groups so formed remain recognizable as species-groups within the genus *Astalotermes*. Having considered the possibility that they could be treated as subgenera, I now think it is better to deal with them informally. They are of value in indicating more clearly the affinities of *Astalotermes* with other genera, but the groups are not so well-defined that any useful purpose would be served by naming them. As usual, there are some species that appear to be related to more than one group and do not readily fall into any of them. The arrangement of the species descriptions following the keys conforms to these general groupings, as indicated below.

Group I. Smaller species, W, (Imago) 0.69–0.86; apical teeth of mandibles longer, L_A/L_1 (Imago) 0.50–0.79, (Worker) 0.56–0.86; imago, meso- and metanota rather consistently narrower at constriction, M/W, 0.20–0.28; worker, enteric valve seating lateral or dorsolateral in unopened abdomen, sessile to strongly necked, weakly to distinctly two-lobed. Species included: *A. amicus* sp. n., *A. benignus* sp. n., *A. comis* sp. n., *A. concilians* (Silvestri), *A. eumenus* sp. n., *A. amicus* and *A. eumenus* have longer apical teeth than the other species. These, and their strongly necked enteric valves may indicate a leaning towards *Acholotermes*. At the other end of the group, *A. comis* is clearly related to *Acidnotermes*.

Group II. Larger species, W, (Imago) 0.98–1.23; apical teeth of mandibles a little shorter in some species, (Imago) 0.55–0.66 (Worker) 0.62–0.79; imago, meso- and metanota variably wider at constriction, M/W, 0.26–0.32; worker, enteric valve seating ventrolateral to lateral in unopened abdomen, long-necked, distinctly two- or three-lobed. Species included: *A. aganus* sp. n., *A. hapalus* sp. n., *A. ignavus* sp. n., *A. mitis* sp. n. and *A. murcus* sp. n. *A. ignavus* and *A. murcus* are more closely related to each other than to the rest, with their extremely long head-setae. The other three species may represent a link with genera such as *Alyscotermes* and perhaps *Astratotermes*. It is also likely that *Adynatotermes* and *Aganotermes* are derived from forms like these.

Group III. Medium-sized to larger species, W, (Imago) 0.76-1.20; apical teeth of mandibles somewhat shorter. L_A/L_1 , (Imago) 0.41-0.64, (Worker) 0.43-0.64; right mandible of worker with anterior edge at first marginal tooth much shorter than that of second; imago, meso- and metanota variably somewhat wider than Group I. M/W, 0.23-0.34; worker enteric valve seating ventro- to dorsolateral in unopened abdomen, sessile or short-necked, weakly two- or three-lobed. Species included: *A. acholus* sp. n., *A. brevior* (Holmgren), *A. obstructus* sp. n., *A. quietus* (Silvestri). This group is the most specialized in the genus, with the distinctly reduced first marginal tooth of the right mandible. This reduction looks like an adaptation to soil-feeding alternative to the commoner form in which the elongated apical tooth becomes widely spaced from the first marginal and the second marginal is reduced. The wide space between the pick-like apical and the second marginal produced by the suppression of the first marginal achieves a similar result. This feature is again found in *Anenteotermes*, and the slightly longer mesenteric overlap with the proctodeum found in Group III may be a further indication of relationship with that genus.

Other Species. Three species do not fit readily into any group. *A. impediens* sp. n. is a medium-sized species which most resembles Group I but has shorter apical teeth to the mandibles and somewhat wider meso- and metanota. The latter feature, with the long necked, rather prominently lobed enteric valve seating, suggest affinities with Group II. *A. empodius* sp. n. is closest to Group II but the strongly lobed sessile, dorsolateral enteric valve seating in the worker and narrow meso- and metanota in the imago add to a general similarity of appearance to *Adynatotermes*, which is borne out by its position in the principal co-ordinates analysis. *A. irrixosus* sp. n., like the previous species, was at first included in Group II, but its larger size, the proportions of the mandibles, the slender fore tibia of the worker and the wider imaginal meso- and metanota suggest affinities with *Astratotermes* and *Alyscotermes*. It also has the enteric valve seating dorso-lateral in the worker abdomen.

KEY TO SPECIES

Imagos

- | | | |
|---|---|------------------------|
| 1 | Right mandible with anterior edge of first marginal tooth at least as long as anterior edge of second marginal (where second marginal connected to posterior edge of first by a continuous curve, lowest point to be regarded as beginning of second) | 2 |
| - | Right mandible with anterior edge of first marginal distinctly shorter than anterior edge of second marginal | 16 |
| 2 | Pilosity of head capsule consists of short somewhat uneven pelt with very long emergent setae, many of them over 0.2 mm; those near compound eyes extending beyond outer curve of eye by nearly half their length | 3 |
| - | Pilosity of head capsule shorter, emergent setae, where distinct, at most only slightly beyond curve of eye | 4 |
| 3 | Meso- and metanota proportionately wider at constriction, M/W, 0.31-0.32 | |
| | | <i>ignavus</i> (p. 75) |
| - | Meso- and metanota narrower at constriction, M/W, 0.26-0.27 | <i>murcus</i> (p. 79) |

- 4 Fontanelle subject to pronounced sexual dimorphism: in ♀, large sunken pale area approximately equal in size to compound eye; in ♂ small black slit or obsolete, surrounded by dark pigmented area larger than ocellus *acholus* (p. 139)
- Fontanelle not so 5
- 5 Left mandible with apical tooth shorter in proportion to distances between marginal teeth, complex ratio $L_A/L_1.L_m$, under 6.5 (known range 4.5–5.5) 6
- Left mandible with apical tooth proportionately longer, $L_A/L_1.L_m$, over 6.5 (known range 7.5–13.2) 7
- 6 Meso- and metanota proportionately wider at constriction, M/W , 0.33–0.36. Left mandible with proximal end of subsidiary marginal tooth separated from molar prominence by wide notch; postclypeus more strongly inflated, Pcl/W , 0.26–0.27, with distinct median suture *irrixosus* (p. 100)
- Meso- and metanota narrower at constriction, M/W , 0.22–0.28. Left mandible with subsidiary marginal tooth only just clear of molar prominence, and with markedly concave cutting edge; postclypeus weakly inflated Pcl/W , 0.22–0.24, median suture indistinct or absent *empodius* (p. 94)
- 7 Ocelli almost touching compound eyes, separated by one-quarter or less of own least diameter *obstructus* (p. 88)
- Ocelli separated from compound eyes by at least one-third own least diameter 8
- 8 Ocelli small and separated from eyes by more than own least diameter *aganus* (p. 69)
- Ocelli larger, separated from eyes by less than own least diameter 9
- 9 Larger, W , 0.98–1.01; meso- and metanota wider at constriction M , 0.29–0.33, N , 0.29–0.33, $L_1/M.N$, 1.40–1.81 10
- Smaller, W , 0.69–0.94; meso- and metanota narrower at constriction, M , 0.14–0.25, N , 0.14–0.28, $L_1/M.N$, 1.99–5.35 11
- 10 Postclypeus more inflated, apical teeth of mandibles shorter, Pcl/R_A , 3.00–3.22, L_A/L_1 , 0.52–0.56 *hapalus* (p. 72)
- Postclypeus less inflated, apical teeth of mandibles longer, Pcl/R_A , 2.61, L_A/L_1 , 0.66 *mltis* (p. 77)
- 11 Postclypeus less inflated, apical teeth of mandibles longer, Pcl/R_A , 1.93–2.00, R_A/R_1 , 1.04–1.05 *amicus* (p. 58)
- Postclypeus more inflated, apical teeth of mandibles shorter, Pcl/R_A , 2.83–4.15, R_A/R_1 , 0.65–0.89 12
- 12 Right mandible with second marginal tooth distinctly broader based and more robust than first, distal margin slightly convex (Text-fig. 74) *comis* (p. 63)
- Right mandible with marginal teeth approximately equal or first more prominent, distal margin of second straight or slightly concave 13
- 13 Fore tibia with third (outer) apical spur, vestigial. Smaller, W , 0.69–0.73 *benignus* (p. 61)
- Fore tibia with third apical spur only slightly smaller than other two. Larger, W , 0.73–0.94 14
- 14 Meso- and metanota proportionately wider at constriction, apical teeth of mandibles slightly shorter, M/R_A , 3.40–3.77, $L_1/M.N$, 1.99–2.32. Larger, W , 0.86–0.94. Compound eyes prominent in proportion to own diameter (Text-fig. 204) *impedians* (p. 98)
- Meso- and metanota narrower at constriction, apical teeth slightly longer, M/R_A , 2.10–3.00, $L_1/M.N$, 2.69–4.13. Smaller, W , 0.73–0.86, compound eyes not prominent in proportion to own diameter 15
- 15 Posterior margin of head capsule evenly rounded. Smaller, W , 0.73–0.75. Left mandible, apical tooth longer, L_A/L_1 , 0.69–0.79, proximal end of subsidiary marginal tooth separated from molar prominence by definite notch (Text-fig. 75) *eumenus* (p. 67)
- Posterior margin of head slightly unevenly rounded. Larger, W , 0.75–0.86. Left mandible, apical tooth shorter, L_A/L_1 , 0.52–0.64, proximal end of subsidiary marginal tooth just clear of molar prominence (Text-fig. 73) *concilians* (p. 65)

- 16 Posterior margin of head capsule usually evenly rounded, pilosity a short fine pelt with emergent setae. Median suture of postclypeus usually weak, sometimes absent. Transverse dark suture of mesonotum weak or absent, that of metanotum weak. (Distribution, West Africa to Uganda, and Congo) *quietus* (p. 91)
- Posterior margin of head capsule usually unevenly rounded, pilosity usually uneven, but occasionally approaching a pelt. Median suture of postclypeus distinct. Transverse sutures of meso- and metanota distinct. (Distribution, S. Africa to Angola) *brevior* (p. 84)

Workers

- 1 Fore tibia with third apical spur vestigial, one-quarter or less length of other two (3rd spur sometimes hard to find) 2
- Fore tibia with third apical spur not vestigial, more than one-quarter length of other two 6
- 2 Small, W, 0.65-0.66. Fore tibia more inflated T_1/T_w , 4.22-4.34. Enteric valve seating dorsolateral, nearly dorsal, in unopened abdomen *benignus* (p. 61)
- Larger, W, 0.85-1.08. Fore tibia less inflated, T_1/T_w , 4.55-5.96. Enteric valve seating lateral in unopened abdomen 3
- 3 Apical teeth of mandibles longer, L_A/L_1 , 0.79; left mandible with proximal end of subsidiary marginal tooth clear of molar prominence but not separated by deep notch, $L_A/L_1.L_m$, 15.81. Postclypeus more inflated, Pcl/R_1 , 3.05. Fore tibia more inflated, T_1/T_w , 4.55. Pilosity of head capsule pale, fine and inconspicuous. Junction between mesenteron and proctodeum nearly transverse; enteric valve seat prominently bilobed, ventrolateral in unopened abdomen (Text-figs 000 & 000) *mitis* (p. 77)
- Apical teeth of mandibles shorter L_A/L_1 , 0.62-0.73; proximal end of subsidiary marginal tooth separated by deep notch from molar prominence, $L_A/L_1.L_m$, 7.90-9.97. Postclypeus less inflated, Pcl/R_1 , 2.39-2.63. Fore tibia less inflated, T_1/T_w , 5.21-5.96. Pilosity of head capsule long, yellow to yellow-brown, conspicuous. Mesenteric-proctodeal junction diagonal or longer, enteric valve seat weakly bilobed, lateral 4
- 4 Right mandible with anterior edge of first marginal tooth shorter than anterior edge of second *murcus* (p. 79)
- Right mandible with anterior edge of first marginal tooth slightly longer than anterior edge of second 5
- 5 Smaller, W, 0.85. Apical teeth of mandibles shorter, L_A/L_1 , 0.62 *ignavus* (p. 75)
- Larger, W, 1.08. Apical teeth of mandibles longer, L_A/L_1 , 0.73 *irrixosus* (p. 100)
- 6 Enteric valve seating sessile on second pouch of proctodeum or at most with very short (length less than own width) neck 7
- Enteric valve seating with a definite to very long (length equal to own least width or more) neck connecting it with second pouch of proctodeum 11
- 7 Right mandible with anterior edge of first marginal tooth approximately equal to anterior edge of second. Enteric valve seating with three prominent lobes, inner almost equal to outer pair *empodius* (p. 94)
- Right mandible with anterior edge of first marginal tooth definitely shorter than anterior edge of second. Enteric valve seating weakly lobed, inner lobe where present much smaller than outer pair 8
- 8 Small, W, 0.58-0.60. Proportions of mandibular teeth by complex ratios $L_A/L_1.L_m$, 14.80-18.60, $R_A/R_1.R_m$, 18.29-22.15. Fore tibia more inflated, T_1/T_w , 3.90-4.07 *comis* (p. 63)
- Larger, W, 0.70-0.93. Mandibular ratios, $L_A/L_1.L_m$, 7.25-12.41, $R_A/R_1.R_m$, 9.94-14.10. Fore tibia less inflated, T_1/T_w , 4.02-5.52 9

- 9 Enteric valve seating ventrolateral in unopened abdomen. Smaller, W , 0.70, T_1 , 0.46, fore tibia more inflated, T_1/T_w , 4.02. 'Abdominal dehiscence' absent
acholus (p. 82)
- Enteric valve seating dorsolateral in unopened abdomen. Larger, W , 0.71–0.93, T_1 , 0.50–0.66, fore tibia less inflated, T_1/T_w , 4.21–5.52. 'Abdominal dehiscence' very frequent 10
- 10 Armature of enteric valve with a few minute spines on the proximal one-third of cushions in positions 3 and 4. (Distribution, South Africa to Angola) *brevior* (p. 84)
- Enteric valve cushions scaly, without spines. (Distribution, W. Africa to Uganda, and Congo) *quietus* (p. 91)
- 11 Larger, W , 0.88–0.91 12
- Smaller, W , 0.64–0.77 13
- 12 Enteric valve seating with two prominent lobes only, lateral in unopened abdomen. Mesenteric-proctodeal junction diagonal *hapalus* (p. 72)
- Enteric valve seating with three prominent lobes, third almost equal, ventrolateral in unopened abdomen. Mesenteric-proctodeal junction nearly transverse
aganus (p. 69)
- 13 Right mandible with anterior edge of first marginal tooth distinctly shorter than anterior edge of second *obstructus* (p. 88)
- Right mandible with anterior edge of first marginal approximately equal to second 14
- 14 Fore tibia more inflated, T_1/T_w , 3.86–3.88. Apical teeth of mandibles longer, L_A/L_1 , 0.69–0.86, R_A/R_1 , 0.97–1.00 15
- Fore tibia less inflated, T_1/T_w , 4.22–4.47. Apical teeth of mandibles shorter, L_A/L_1 , 0.54–0.67. R_A/R_1 , 0.72–0.92 16
- 15 Larger, W , 0.77, T_1 , 0.61. Left mandible with subsidiary marginal tooth just clear of molar prominence. Complex ratio $R_A/T_w.L_1$, 4.46 *amicus* (p. 58)
- Smaller, W , 0.64, T_1 , 0.43. Left mandible with subsidiary marginal tooth separated from molar prominence by deep notch. Complex ratio $R_A/T_w.L_1$, 7.20
eumenus (p. 67)
- 16 Apical teeth of mandibles proportionately shorter, L_A/L_1 , 0.54; left mandible with subsidiary marginal tooth separated from molar prominence by deep notch, $L_A/L_1.L_m$, 12.45. (Distribution, Zambia) *impedians* (p. 98)
- Apical teeth proportionately longer, L_A/L_1 , 0.59–0.67; left mandible with subsidiary marginal tooth just clear of molar prominence, $L_A/L_1.L_m$, 15.65–17.79. (Distribution, West Africa) *concilians* (p. 65)

Group I

Astalotermes amicus sp. n.

(Text-figs 57, 58, 67, 68 & 77–82; Pl. I, fig. 4)

Imago. Head capsule brown, not darker above ocelli; fontanelle small, about one-third size of ocellus, roughly circular with small depression in middle, pale yellow-brown; medial spot roughly circular, flat or slightly raised, little smaller than fontanelle, yellow-brown; postclypeus yellow-brown, labrum yellow; frontal marks flat, almost obsolete, weak crescents, yellow-brown; antennae yellow. Pronotum, meso- and metanota yellow-brown, transverse sutures present but weak; legs, femora yellow, tibiae pale yellow, tarsi yellow-white. Abdominal tergites yellow-brown, sternites, dorsal and ventral stigmata pale yellow-brown, cerci pale yellow.

Posterior margin of head capsule evenly rounded; ocelli medium-sized, separated from compound eyes by half own least diameter or slightly more; postclypeus moderately inflated, Pcl/W , 0.25–0.26, Pcl/R_A , 1.93–2.00, posterior margin evenly rounded, median suture very weak. Apical teeth of mandibles rather long, L_A/L_1 , 0.71–0.79, R_A/R_1 , 1.04–1.05; subsidiary

marginal tooth of left mandible with proximal end just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 11.61-13.20; points of apical and marginal teeth of right mandible in line, anterior edges of marginal teeth approximately equal. Pilosity of head capsule yellow, slightly uneven, nearly a rough pelt with emergent setae. Fore tibia with third spur distinct.

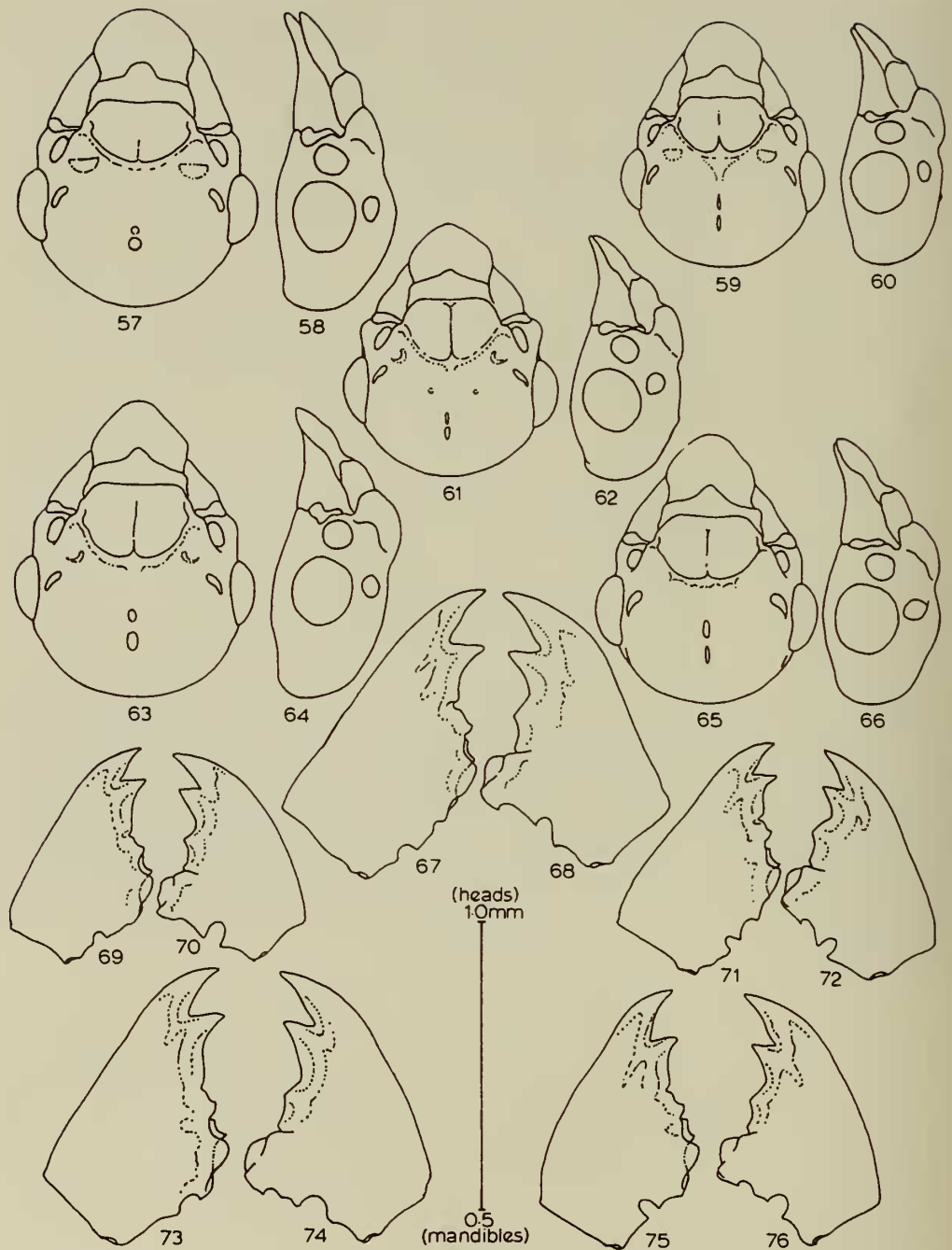
Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	0.80-0.82
Ocellus ($O_w \times O_l$)	0.07 \times 0.09
Ocellus to eye (O-E)	0.03-0.04
Postclypeus length (Pcl)	0.20-0.21
Antennal article III	0.03-0.04
Antennal article IV	0.04-0.05
Antennal article V	0.04-0.06
Left mandible, apical to first marginal (L_A)	0.09-0.10
Left mandible, first to third marginal (L_1)	0.13
Left mandible, third marginal to molar (L_m)	0.06
Right mandible, apical to first marginal (R_A)	0.10-0.11
Right mandible, first to second marginal (R_1)	0.10
Right mandible, second marginal to molar (R_m)	0.06
Mesonotum width (M)	0.16-0.23
Metanotum width (N)	0.15-0.23

Worker. Head capsule pale yellow, pilosity similarly coloured, very fine, silky and sparse. Postclypeus rather weakly inflated, Pcl/W , 0.24, Pcl/R_1 , 2.10. Apical teeth of mandibles rather long, L_A/L_1 , 0.69, R_A/R_1 , 0.97; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 14.45; first marginal tooth of right mandible slightly behind line of apical to second marginal, but anterior edge equal to that of second, $R_A/R_1.R_m$, 20.99. Fore tibia moderately inflated, T_1/T_w , 3.86, third apical spur distinct. Mesenteric junction with proctodeum diagonal, to right of malpighian knot; enteric valve seating lateral in unopened abdomen, two lobes moderately developed, connected to second pouch by proctodeum by long neck, membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (one specimen) in millimetres.

Head width (W)	0.77
Fore tibia width (T_w)	0.16
Fore tibia length (T_1)	0.61
Postclypeus length (Pcl)	0.18
Left mandible, apical to first marginal (L_A)	0.08
Left mandible, first to third marginal (L_1)	0.12
Left mandible, third marginal to molar (L_m)	0.05
Right mandible, apical to first marginal (R_A)	0.09
Right mandible, first to second marginal (R_1)	0.09
Right mandible, second marginal to molar (R_m)	0.05



FIGS 57-76. *Astalotermes*, imago head capsules, front and side views, and imago mandibles. 57, 58 & 67, 68, *A. amicus*; 59, 60 & 69, 70, *A. benignus*; 61, 62 & 71, 72, *A. comis*; 63, 64 & 73, 74, *A. concilians*; 65, 66 & 75, 76, *A. eumenus*.

This species is separable from its nearest relations, *A. comis* sp. n., *A. concilians* (Silvestri) and *A. eumenus* sp. n. in the imago by its weakly inflated postclypeus and longer apical teeth of the mandibles. The worker is larger than *A. comis* and *A. eumenus*, with differently proportioned mandibles, and in *A. concilians* the fore tibia is less inflated and the apical teeth shorter. The abdomen of the worker caste does not appear to be dehiscent in *A. amicus*.

Holotype ♀ imago, paratype ♀ and ♂ imagos, and workers from type-colony, TANZANIA: Amani, 21.iv.1950 (*P. B. Kemp* Coll. No. 384), in British Museum (Natural History).

Only the type nest-series of this species is known.

There is no information on its biology.

Astalotermes benignus sp. n.

(Text-figs 59, 60, 69, 70 & 83-88; Pl. I, fig. 3)

[*Anoplotermes lateralis* (Walker); Silvestri, 1914 : 65. Misidentification.]

Imago. Head capsule dark sepia-brown, very dark above ocelli; fontanelle small, brown, elongate oval, weakly ridged in middle, running forwards into groove through medial spot; medial spot sepia-brown, oval, slightly ridged on each side of groove that continues forward into depressed triangular area behind postclypeus; postclypeus sepia-brown, labrum yellow-brown; frontal marks brown, semicircular, distinct, very slightly depressed; antennae brown. Pronotum, meso- and metanota sepia-brown, transverse dark sutures present; legs, femora and tibiae yellow-brown, tarsi yellow. Abdominal tergites brown, with sepia-brown stigmata, sternites pale brown with brown stigmata; cerci pale brown.

Posterior margin of head capsule evenly rounded; ocelli medium-sized, separated from compound eyes by two-fifths to two-thirds own least diameter; postclypeus moderately inflated, Pcl/W, 0.26-0.30, Pcl/R_A, 3.06-3.63, posterior margin evenly rounded, median suture weak, absent anteriorly. Apical teeth of mandibles short, L_A/L₁, 0.50-0.57, R_A/R₁, 0.71-0.82; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, L_A/L₁.L_m, 11.13-12.40; points of apical and marginal teeth of right mandible in line, anterior edges of marginal teeth equal. Pilosity of head capsule yellow-brown, very uneven, no pelt. Fore tibia with vestigial third spur sometimes extremely difficult to find.

Measurements (three specimens from two localities) in millimetres.

	Range	Mean
Head width across eyes (W)	0.69-0.73	0.705
Ocellus (O _w × O _l)	0.05-0.06 × 0.07-0.08	0.055 × 0.077
Ocellus to eye (O-E)	0.02-0.03	0.030
Postclypeus length (Pcl)	0.19-0.21	0.195
Antennal article III	0.03	—
Antennal article IV	0.03-0.04	0.033
Antennal article V	0.03-0.04	0.033
Left mandible, apical to first marginal (L _A)	0.06	—
Left mandible, first to third marginal (L ₁)	0.10-0.11	0.107
Left mandible, third marginal to molar (L _m)	0.04-0.05	0.046

Right mandible, apical to first marginal (R_A)	0.06	—
Right mandible, first to second marginal (R_1)	0.08	—
Right mandible, second marginal to molar (R_m)	0.05	—
Mesonotum width (M)	0.15-0.18	0.165
Metanotum width (N)	0.14-0.19	0.166

Worker. Head capsule yellow, pilosity orange-yellow, numerous and rather coarse, short. Postclypeus rather strongly inflated, Pcl/W , 0.29-0.30, Pcl/R_1 , 2.35-2.55. Apical teeth of mandibles fairly short, L_A/L_1 , 0.58-0.61, R_A/R_1 , 0.71-0.80; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, $L_A/L_1.L_m$, 15.19-16.50; apical and marginal teeth of right mandible approximately in line, anterior edges of marginal teeth equal, $R_A/R_1.R_m$, 19.00-19.39. Fore tibia weakly inflated, T_1/T_w , 4.22-4.34, third apical spur vestigial. Mesenteric junction with proctodeum slightly longer than diagonal, to right of malpighian knot; enteric valve seating dorsolateral in unopened abdomen, weakly two-lobed, connected to second pouch of proctodeum by short neck, membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (two specimens from two localities) in millimetres.

Head width (W)	0.65-0.66
Fore tibia width (T_w)	0.10
Fore tibia length (T_1)	0.43-0.44
Postclypeus length (Pcl)	0.19
Left mandible, apical to first marginal (L_A)	0.06
Left mandible, first to third marginal (L_1)	0.10
Left mandible, third marginal to molar (L_m)	0.04
Right mandible, apical to first marginal (R_A)	0.06
Right mandible, first to second marginal (R_1)	0.08
Right mandible, second marginal to molar (R_m)	0.04

The vestigial third apical spur of the fore tibia distinguishes this small species from its closest relatives, *A. concilians* in particular since it is sympatric. The other species with a vestigial spur are much larger in Group II, and *A. benignus* is in any case unique in the genus in having the spur reduced to this extent in both castes. It also differs from *A. amicus* and *A. eumenus*, and *A. comis* in the proportions of the mandibular teeth. The abdomen of the worker is definitely dehiscent in *A. benignus*.

Holotype ♀ imago, paratype ♀ and ♂ imagos, and workers from type-colony, GUINEA: Mt. Nimba, Pierré Richaud, 10.viii.1951 (*M. Lamotte* coll. No. 18 Pa.392), in American Museum of Natural History (paratype ♀ and worker from type-colony also in BMNH).

Other paratype material. GUINEA: Mamou, 10°20'N., 12°15'W., 25.viii.1912

(*F. Silvestri*), in Silvestri Coll., Ist. Ent. Agr. Portici, and AMNH. IVORY COAST: Mt. Nimba, 26.xii.1968 (*G. Josens*), in his own collection and BMNH.

The existing records provide no information on the biology of this species.

Astalotermes comis sp. n.

(Text-figs 61, 62, 71, 72 & 89-94)

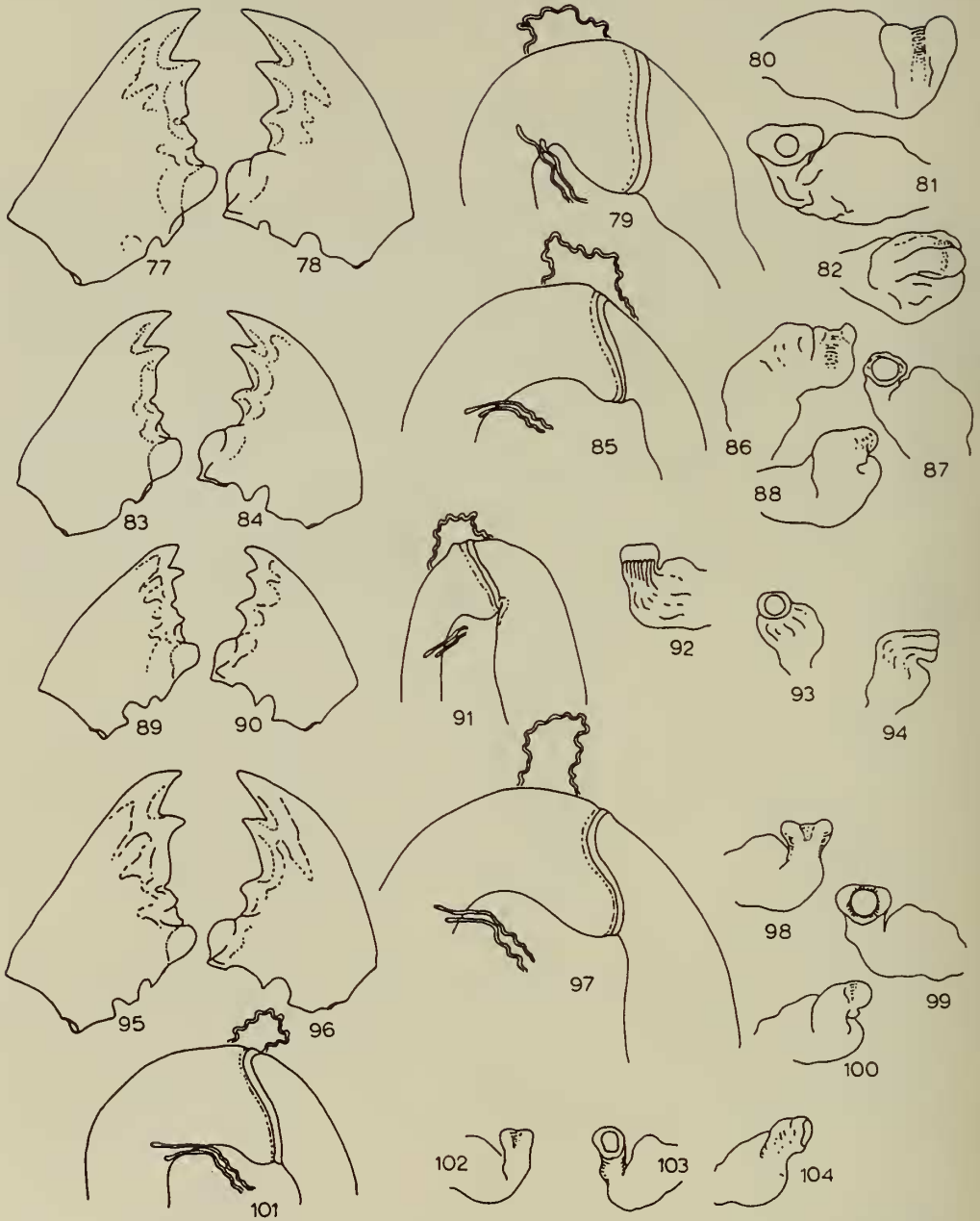
Imago. Head capsule sepia-brown, dark sepia-brown above ocelli, dark areas usually extending as tapering streaks converging to fontanelle; fontanelle small, oval, flat, indistinct, coloured as head; medial spot elongate oval, about as large as fontanelle, also coloured as head; postclypeus brown, labrum pale brown; frontal marks weak flat crescents, brown; antennae, pale brown. Pronotum brown, meso- and metanota pale brown, transverse dark suture weak on meso-, distinct on metanotum; legs, femora and tibiae pale brown, tarsi yellow-white. Abdominal tergites and lateral parts of sternites pale brown, middle of sternites yellow-white, stigmata as sclerites; cerci yellow-white.

Posterior margin of head capsule not quite evenly rounded, slightly undulating, ocelli medium-sized, separated from compound eyes by from two-fifths to three-quarters own least diameter; postclypeus moderately inflated, Pcl/W , 0.27-0.31, Pcl/R_A , 3.21-4.15, posterior margin evenly rounded, median suture distinct. Apical teeth of mandibles short, L_A/L_1 , 0.51-0.63, R_A/R_1 , 0.65-0.82; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, $L_A/L_1.L_m$, 8.66-10.91; point of right first marginal tooth slightly behind line from apical to second marginal, and its anterior edge slightly shorter than that of broadly based second. Pilosity of head capsule brown, dense, uneven, no pelt. Fore tibia with well developed third apical spur.

Measurements (nine specimens from five localities) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	0.69-0.81	0.736 \pm 0.040
Ocellus ($O_w \times O_1$) . . .	0.06-0.08 \times 0.08-0.10	0.064 \pm 0.005 \times 0.085 \pm 0.010
Ocellus to eye (O-E) . . .	0.03-0.05	0.039 \pm 0.006
Postclypeus length (Pcl) . . .	0.19-0.25	0.210 \pm 0.002
Antennal article III . . .	0.02-0.03	0.019 \pm 0.003
Antennal article IV . . .	0.02-0.04	0.028 \pm 0.006
Antennal article V . . .	0.02-0.04	0.027 \pm 0.005
Left mandible, apical to first marginal (L_A) . . .	0.05-0.07	0.053 \pm 0.007
Left mandible, first to third marginal (L_1) . . .	0.09-0.11	0.095 \pm 0.008
Left mandible, third marginal to molar (L_m) . . .	0.05-0.06	0.057 \pm 0.003
Right mandible, apical to first marginal (R_A) . . .	0.05-0.07	0.057 \pm 0.008
Right mandible, first to second marginal (R_1) . . .	0.07-0.09	0.078 \pm 0.006
Right mandible, second marginal to molar (R_m) . . .	0.05-0.06	0.052 \pm 0.004
Mesonotum width (M) . . .	0.14-0.20	0.163 \pm 0.020
Metanotum width (N) . . .	0.14-0.21	0.162 \pm 0.027

Worker. Head capsule yellow-white, pilosity same colour, very sparse, fine, and short. Postclypeus strongly inflated, Pcl/W , 0.32-0.35, Pcl/R_1 , 3.04-3.95. Apical teeth of mandibles fairly short, L_A/L_1 , 0.56-0.61, R_A/R_1 , 0.69-0.80; subsidiary marginal tooth of left mandible



FIGS 77-104. *Astalotermes*, worker mandibles, mesenteric-proctodeal junctions showing attachments of malpighian tubules and positions of malpighian knot, and views of enteric valve seatings. 77-82, *A. amicus*; 83-88, *A. benignus*; 89-94, *A. comis*; 95-100, *A. concilians*; 101-104, *A. eumenus*.

just clear of molar prominence in surface view, $L_A/L_1.L_m$, 14.8-18.6; point of right first marginal tooth slightly behind line from apical to second marginal, and its anterior edge distinctly shorter than that of broadly-based second, $R_A/R_1.R_m$, 18.29-22.15. Fore tibia moderately inflated, T_1/T_w , 3.90-4.07, third apical spur prominent. Mesenteric junction with proctodeum almost transverse, coinciding with malpighian knot; enteric valve seating lateral in unopened abdomen, very weakly two-lobed, almost a rim, sessile on second pouch of proctodeum, membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (four specimens from three localities) in millimetres.

	Range	Mean
Head width (W)	0.58-0.60	0.585
Fore tibia width (T_w)	0.10-0.11	0.105
Fore tibia length (T_1)	0.41-0.43	0.422
Postclypeus length (Pcl)	0.18-0.20	0.192
Left mandible, apical to first marginal (L_A)	0.04-0.05	0.045
Left mandible, first to third marginal (L_1)	—	0.077
Left mandible, third marginal to molar (L_m)	0.03-0.04	0.034
Right mandible, apical to first marginal (R_A)	0.04-0.05	0.043
Right mandible, first to second marginal (R_1)	0.05-0.06	0.056
Right mandible, second marginal to molar (R_m)	—	0.038

A. comis is distinguishable from near relations such as *A. amicus*, *A. concilians* and *A. eumenus* in both castes by the broadly based second marginal and smaller first marginal of the right mandible. Differences from *A. benignus* and *Acidnotermes praus* are given under those species, and its relationship to the latter has already been discussed. The reduced right first marginal tooth in the worker perhaps also indicates a trend towards the Group III species. However, the proportions of the mandibles are actually different, as indicated by the complex ratios, and the mesenteric junction with the proctodeum is shorter. A further feature is that the worker abdomen appears non-dehiscent in *A. comis*.

Holotype ♀ imago, paratype ♀ and ♂ imagos, and workers from type-colony, REPUBLIC OF SOUTH AFRICA: Natal, Ubombo, 18.xi.1955 (*W. G. H. Coaton*) in National Collection of Isoptera, No. TM. 1413, Pretoria. (Paratype ♀ and ♂ imagos, and workers from type-colony also in British Museum (Natural History).)

Other paratype material. REPUBLIC OF SOUTH AFRICA: Natal, Ubombo, 18, 19, 21.xi.1955, six vials, Ingwavuma, 23.xi.1955, two vials, Transvaal, Waterberg, 3.x.1960 (*W. G. H. Coaton*) in N.C.I., Pretoria and BMNH.

A total of 10 nest-series have been examined, but no information is available on the biology of this species.

Astalotermes concilians (Silvestri) comb. n.

(Text-figs 63, 64, 73, 74 & 95-100)

Anoplotermes concilians Silvestri, 1914 : 59. LECTOTYPE ♀, GUINEA: Kindia (Silvestri Coll., Istituto di Entomologia Agraria, Naples), here designated [examined].

Anoplotermes placidus Silvestri, 1914 : 63. LECTOTYPE ♂, GUINEA: Mamou (Silvestri Coll., Istituto di Entomologia Agraria, Naples), here designated [examined]. **Syn. n.**

Imago. Head capsule brown to sepia-brown, very dark above ocelli; fontanelle small, yellow-brown to pale brown, short oval, slightly depressed; medial spot short oval, flat or slightly

raised, coloured as head; postclypeus yellow-brown to sepia-brown, not darker than head capsule, labrum pale yellow-brown to pale brown; frontal marks smooth, pale, flat, crescents, yellow-brown to brown; antennae pale yellow-brown. Pronotum, meso- and metanota, yellow-brown to brown, transverse dark sutures weak on meso- and metanota; legs, femora pale yellow-brown to pale brown, tibiae paler, tarsi yellow-white to yellow. Abdominal tergites and lateral parts of sternites brown, proximal three sternites paler in middle, dorsal stigmata sometimes paler than tergites, ventral stigmata pale brown; cerci yellow-white.

Posterior margin of head capsule not quite evenly rounded, slightly undulating; ocelli medium-sized, separated from compound eyes by from two-fifths to two-thirds own least diameter; postclypeus moderately to strongly inflated, Pcl/W , 0.27-0.36, Pcl/R_A , 2.83-3.43, posterior margin evenly rounded, median suture distinct. Apical teeth of mandibles short L_A/L_1 , 0.52-0.64, R_A/R_1 , 0.71-0.88; subsidiary marginal tooth of left mandible clear of molar prominence in surface view, $L_A/L_1.L_m$, 8.51-12.53; points of apical and marginal teeth of right mandible approximately in line, anterior edges of marginal teeth equal or first slightly longer than second. Pilosity of head capsule pale yellow to yellow, uneven, no pelt. Fore tibia with well developed third apical spur.

Measurements (eight specimens from six localities) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	0.75-0.86	0.812 \pm 0.039
Ocellus ($O_w \times O_1$) . . .	0.06-0.08 \times 0.08-0.10	0.066 \pm 0.006 \times 0.089 \pm 0.005
Ocellus to eye (O-E) . . .	0.03-0.04	0.035 \pm 0.004
Postclypeus length (Pcl) . . .	0.21-0.28	0.255 \pm 0.026
Antennal article III . . .	0.02-0.04	0.030 \pm 0.007
Antennal article IV . . .	0.04-0.05	0.043 \pm 0.003
Antennal article V . . .	0.04-0.05	0.044 \pm 0.005
Left mandible, apical to first marginal (L_A) . . .	0.07-0.09	0.079 \pm 0.006
Left mandible, first to third marginal (L_1) . . .	0.12-0.15	0.136 \pm 0.009
Left mandible, third marginal to molar (L_m) . . .	0.05-0.06	0.055 \pm 0.005
Right mandible, apical to first marginal (R_A) . . .	0.07-0.09	0.082 \pm 0.006
Right mandible, first to second marginal (R_1) . . .	0.09-0.12	0.104 \pm 0.011
Right mandible, second marginal to molar (R_m) . . .	0.05-0.06	0.055 \pm 0.004
Mesonotum width (M) . . .	0.19-0.23	0.203 \pm 0.015
Metanotum width (N) . . .	0.18-0.22	0.201 \pm 0.013

Worker. Head capsule yellow-white, pilosity yellow, rather long but sparsely scattered. Postclypeus moderately to strongly inflated, Pcl/W , 0.25-0.35, Pcl/R_1 , 1.69-3.00. Apical teeth of mandibles fairly short to rather longer, L_A/L_1 , 0.59-0.67, R_A/R_1 , 0.72-0.92; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 15.65-17.79; first marginal tooth of right mandible very slightly behind line of apical to second marginal, anterior edge of first marginal approximately equal to that of second, at most only very slightly shorter, $R_A/R_1.R_m$, 16.50-21.00. Fore tibia rather weakly inflated, T_1/T_w , 4.22-4.46, third apical spur prominent, only slightly less than other two. Mesenteric junction with proctodeum diagonal, sinuate, to right of malpighian knot, distal end of mesenteron slightly swollen; enteric valve seating lateral in unopened abdomen, clearly two-lobed with sometimes a trace of third, inner lobe, connected to second pouch of proctodeum by distinct neck, membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (three specimens from three localities) in millimetres.

	Range	Mean
Head width (W)	0.66-0.71	0.692
Fore tibia width (T _w)	0.10-0.11	0.107
Fore tibia length (T _l)	0.45-0.48	0.463
Postclypeus length (Pcl)	0.17-0.24	0.196
Left mandible, apical to first marginal (L _A)	0.07-0.08	0.073
Left mandible, first to third marginal (L ₁)	0.11-0.13	0.118
Left mandible, third marginal to molar (L _m)	—	0.038
Right mandible, apical to first marginal (R _A)	0.07-0.08	0.073
Right mandible, first to second marginal (R ₁)	0.08-0.10	0.090
Right mandible, second marginal to molar (R _m)	0.04-0.05	0.044

The differences between *A. concilians* and *A. amicus*, *A. benignus* and *A. comis* have already been given under those species. Within Group I there only remains *A. eumenus*. This species is very similar, though slightly smaller, with somewhat longer apical teeth to the mandibles in both imago and worker castes; the latter has also a more inflated fore tibia. The abdomen of the worker is definitely desiccant in *A. concilians*.

Lectotypes have been designated from the existing syntype material of *A. concilians* (Silvestri) and *A. placidus* (Silvestri) as indicated below.

Type-material. *Anoplotermes concilians* Silvestri, LECTOTYPE ♀ imago, paralectotype ♀ imagos and workers from type-colony, GUINEA: Kindia, 10°N., 12°45'W., 21.viii.1912 (*F. Silvestri*), in Silvestri Coll., Istituto di Entomologia Agraria, Portici, Naples. *Anoplotermes placidus* Silvestri, LECTOTYPE ♂ imago, paralectotype ♀ (teneral) and ♂ imagos and workers from type-colony, GUINEA: Mamou, 10°20'N., 12°15'W., 25.viii.1912 (*F. Silvestri*), in Silvestri Coll., Istituto di Entomologia Agraria, Portici, Naples.

Other material. NIGERIA: Eastern Region; Port Harcourt, 5.iii.1957 (*W. Wilkinson*). Northern Region; 18 m. from Gombe on Numan Road, and 40 m. S.E. of Gombe on Numan Road, 11.v.1957, 20 m. from Yandev on Makurdi Road, 25.ii.1958, two vials (*W. A. Sands*). Apart from the type-series, material is in the BMNH.

A total of seven nest-series have been examined. Those for which the information is available suggest that this species is commonly found in the nests or mounds of other termites.

Astalotermes eumenus sp. n.

(Text-figs 65, 66, 75, 76 & 101-104)

Imago. Colour probably faded during long preservation of only known nest-series. Head capsule yellow-brown, not darker above ocelli; fontanelle oval, flat, vestigial, slightly paler than head; medial spot similar in size and shape to fontanelle, colour as head; postclypeus pale yellow-brown, labrum yellow; frontal marks indistinct flat crescents coloured as head; antennae yellow. Pronotum, meso- and metanota pale yellow-brown, transverse sutures absent from meso- and metanota; legs, femora yellow, tibiae and tarsi paler. Abdominal tergites and dorsal stigmata pale yellow-brown. Sternites and ventral stigmata paler still, cerci yellow.

Posterior margin of head capsule evenly rounded; ocelli medium-sized, separated from compound eyes by less than two-fifths own least diameter; postclypeus moderately inflated, Pcl/W , 0.30–0.31, Pcl/R_A , 2.90, posterior margin evenly rounded, median suture present but not strong. Apical teeth of mandibles rather long, L_A/L_1 , 0.69–0.79, R_A/R_1 , 0.85–0.89; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio $L_A/L_1.L_m$, 11.00–12.60; point of right first marginal tooth slightly behind line from apical to second marginal, but anterior edges of marginal teeth equal. Pilosity of head capsule yellow-brown, dense and uneven, no pelt. Fore tibia with third apical spur only slightly smaller than other two.

Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	0.73–0.75
Ocellus ($O_w \times O_1$)	0.06–0.07 \times 0.09
Ocellus to eye (O–E)	0.03
Postclypeus length (Pcl)	0.23
Antennal article III	0.03
Antennal article IV	0.04
Antennal article V	0.04
Left mandible, apical to first marginal (L_A)	0.08
Left mandible, first to third marginal (L_1)	0.10–0.11
Left mandible, third marginal to molar (L_m)	0.06
Right mandible, apical to first marginal (R_A)	0.08
Right mandible, first to second marginal (R_1)	0.09
Right mandible, second marginal to molar (R_m)	0.06
Mesonotum width (M)	0.16–0.17
Metanotum width (N)	0.16

Worker. Head capsule and its pilosity yellow, the latter very sparse. Postclypeus strongly inflated, Pcl/W , 0.35, Pcl/R_1 , 3.21; apical teeth of mandibles long, L_A/L_1 , 0.86, R_A/R_1 , 1.00; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio $L_A/L_1.L_m$, 17.08; first marginal tooth of right mandible slightly behind line of apical to second marginal, but anterior edge equal to that of second, $R_A/R_1.R_m$, 22.15. Fore tibia moderately inflated, T_1/T_w , 3.88, third apical spur pale and about half length of other two. Mesenteric junction with proctodeum diagonal, slightly sinuate, just to right of malpighian knot; enteric valve seating very weakly two-lobed, almost a rim, connected to second pouch of proctodeum by a definite neck, probably lateral in position in unopened abdomen; membranous wall of valve beyond cushions with minute spicules.

Measurements (one specimen) in millimetres.

Head width (W)	0.64
Fore tibia width (T_w)	0.11
Fore tibia length (T_1)	0.43
Postclypeus length (Pcl)	0.23
Left mandible, apical to first marginal (L_A)	0.08
Left mandible, first to third marginal (L_1)	0.09
Left mandible, third marginal to molar (L_m)	0.05
Right mandible, apical to first marginal (R_A)	0.07

Right mandible, first to second marginal (R ₁)	0.07
Right mandible, second marginal to molar (R _m)	0.05

A. eumenus has been compared with the other members of species Group I under their own descriptions and thus no further comment on *A. amicus*, *A. benignus*, *A. comis* and *A. concilians* will be made. Its position in relation to other members of the genus has also been discussed. Whether or not the worker abdomen is dehiscent is uncertain in *A. eumenus*.

Holotype ♀ imago, paratype ♀ and ♂ imagos, and worker from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Mukimbungu, 5°S., 14°E., ix.1909 (*K. E. Laman*), in American Museum of Natural History. Paratype ♀ and ♂ imago from type-colony also in BMNH.

Only the type nest-series is known. There is no information on its biology.

Group II

Astalotermes aganus sp. n.

(Text-figs 106, 107, 116, 117 & 126-131)

Imago. Head capsule dark sepia-brown, slightly darker above ocelli; fontanelle distinct, pale brown to brown, broad oval or nearly circular, distinctly depressed and roughened with irregular transverse striations, only slightly smaller than ocelli; medial spot oval, brown to sepia-brown, flat, slightly smaller than fontanelle; postclypeus sepia brown, labrum pale yellow-brown; frontal marks distinct, semicircular, slightly to distinctly depressed, sepia-brown; antennae, brown. Pronotum sepia-brown, meso- and metanota brown, transverse dark sutures present in both; legs, femora brown, tibiae pale brown, tarsi yellow-white. Abdominal tergites brown, dorsal stigmata sepia-brown, sternites brown, very pale in middle, ventral stigmata brown; cerci pale brown.

Posterior margin of head capsule evenly rounded; ocelli rather small, separated from compound eyes by up to one-third more than own least diameter; postclypeus moderately inflated, Pcl/W, 0.25-0.26, Pcl/R_A, 2.71-2.75, posterior margin evenly rounded, median suture distinct. Apical teeth of mandibles fairly short, L_A/L₁, 0.65-0.66, R_A/R₁, 0.89-0.91; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio L_A/L₁.L_m, 7.47-8.83; points of apical and marginal teeth of right mandible in line, anterior edge of first marginal distinctly longer than that of second. Pilosity of head capsule pale brown, uneven, no pelt. Meso- and metanota somewhat wider at constriction, M/W, 0.27-0.32. Fore tibia with third apical spur distinct.

Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	1.06-1.14
Ocellus (O _w × O _l)	0.08 × 0.10
Ocellus to eye (O-E)	0.09-0.10
Postclypeus length (Pcl)	0.28-0.29
Antennal article III	0.03-0.04
Antennal article IV	0.05-0.06
Antennal article V	0.05-0.06
Left mandible, apical to first marginal (L _A)	0.10-0.11

Left mandible, first to third marginal (L_1)	0.16
Left mandible, third marginal to molar (L_m)	0.08-0.09
Right mandible, apical to first marginal (R_A)	0.10-0.11
Right mandible, first to second marginal (R_1)	0.11-0.12
Right mandible, second marginal to molar (R_m)	0.08
Mesonotum width (M)	0.29-0.36
Metanotum width (N)	0.31-0.38

Worker. Head capsule yellow-white, pilosity pale yellow, very sparse and fine. Postclypeus moderately inflated, Pcl/W , 0.27, Pcl/R_1 , 3.08; apical teeth of mandibles moderately long, L_A/L_1 , 0.75, R_A/R_1 , 1.08; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio $L_A/L_1.L_m$, 14.95; apical and marginal teeth of right mandible approximately in line, anterior margins of first and second marginals equal, $R_A/R_1.R_m$, 19.10. Fore tibia scarcely inflated, T_1/T_w , 4.52, third apical spur distinct though smaller than other two. Mesenteric junction with proctodeum almost transverse, to right of malpighian knot; enteric valve seating ventrolateral in unopened abdomen, prominently three-lobed, third lobe almost equal in size to outer two, connected to second pouch of proctodeum by moderately long neck; membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (one specimen) in millimetres.

Head width (W)	0.91
Fore tibia width (T_w)	0.14
Fore tibia length (T_1)	0.65
Postclypeus length (Pcl)	0.25
Left mandible, apical to first marginal (L_A)	0.10
Left mandible, first to third marginal (L_1) .	0.13
Left mandible, third marginal to molar (L_m)	0.05
Right mandible, apical to first marginal (R_A)	0.09
Right mandible, first to second marginal (R_1)	0.08
Right mandible, second marginal to molar (R_m)	0.06

The *Astalotermes* species of Group II are not so clearly separable from other genera as Group I. *A. aganus* is based on a single nest-series which was at first included in *A. empodius* sp. n. It differs in the proportions of the mandibles, particularly the subsidiary marginal tooth of the left, and in the imago in having smaller ocelli further from the compound eyes; in addition the meso- and metanota are wider at the constriction. In the worker caste, the gut of *A. aganus* is shorter, the enteric valve seating being nearly ventral, and necked, instead of dorsolateral and nearly sessile as in *A. empodius*, which also has a very small third apical spur on the fore tibia. The differences in the proportions of the ocelli and mandibles were sharply pointed up by the principal component scores and the wide separation of the species

in the canonical variates analysis. In the principal component analysis, the transformation vectors corresponding to the second and third latent roots gave the clearest separation. These respectively were composed mainly of a contrast between ocellus size and mandibular tooth length, and a contrast between mandibles and antennal segment lengths. The same characters in different combinations received the largest weightings in the first three imago canonical variates. Apart from the complex ratios already adopted throughout this work as a result of the multivariate analyses, one further is therefore helpful in the present discussion: $O_1 \cdot O_w / L_A \cdot R_A$, *A. aganus*, 0.66–0.72, *A. empodius*, 1.25–1.85.

Of the other members of Group II, *A. ignavus* sp. n. and *A. murcus* sp. n. are distinguished by the very long head setae of the imago, the much shorter postclypeus, and ocelli closer to the compound eyes. In the worker caste, the vestigial third apical spur of the more slender fore tibia and the two-lobed seating of the enteric valve separate these species from *A. aganus*. The same features of the worker, apart from the thickness of the fore tibia, also distinguish *A. mitis* which is rather similar to *A. aganus* in the imago, though with ocelli closer to the eye, and a less evenly rounded posterior margin to the postclypeus. *A. hapalus* resembles *A. mitis* in both castes except that the worker fore tibia has a longer third apical spur, the mandibles have shorter apical teeth, and the postclypeus is longer in the imago. The last two species mentioned appear to be most closely related to *A. aganus* and one another. In the imago of *A. aganus* the fontanelle provides a useful 'spot' character by which it is quickly separated from sympatric members of other genera. *Alyscotermes kilimandjaricus* (Sjöstedt), *Adynatotermes moreletae* (Fuller), *Agano-*

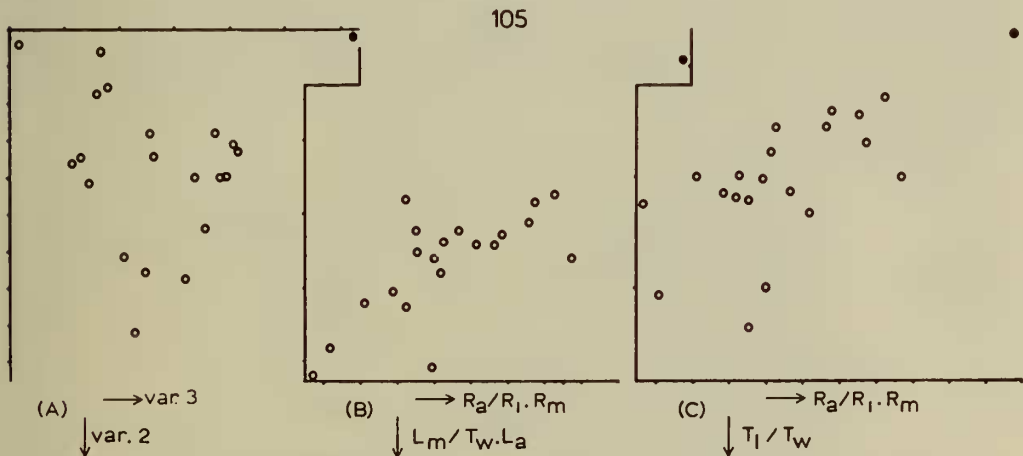


FIG. 105. *Astalotermes hapalus* (solid dot) recognized by computer as distinct in worker caste from *Alyscotermes kilimandjaricus* (rings) after misidentification. (A) Plot of principal component scores (transformed variables) corresponding to latent roots 2 & 3 of correlation matrix. (B) & (C) Plots of discriminant ratios derived from examination of weighting coefficients on original variables provided by eigenvectors of correlation matrix.

termes oryctes sp. n. are all about the same size, and though many other differences are used in keys and descriptions, the fontanelle is easily observed. It is not however a character that can be used more widely since it only differs in degree of development from some congeners mentioned above. Whether or not the worker abdomen is dehiscent is uncertain in *A. aganus*.

Holotype ♀ imago, paratype ♀ and ♂ imagos and workers from type-colony, REPUBLIC OF SOUTH AFRICA: Natal, Mahlabatini, 6.xii.1959 (*P. C. Joubert*) in National Collection of Isoptera, No. TM.6995, Pretoria. (Paratype ♀ and ♂ imagos, and workers from type-colony also in BMNH.)

No biological information is available about the single known nest-series.

Astalotermes hapalus sp. n.

(Text-figs 105, 108, 109, 118, 119 & 132-137)

Imago. Head capsule chestnut-brown, not darker above ocelli, fontanelle less than half as long as ocellus, oval, flat or slightly raised, pale yellow-brown; medial spot nearly circular, flat, same size as fontanelle, brown; postclypeus brown, labrum yellow-brown; frontal marks distinct, crescent-shaped, slightly depressed, pale brown; antennae yellow-brown. Pronotum brown, meso- and metanota brown, transverse dark sutures present in both, stronger in metanotum; legs, femora brown, tibiae yellow-brown, tarsi yellow. Abdominal tergites brown, dorsal stigmata pale brown, sternites pale brown, pale yellow in middle, ventral stigmata pale brown; cerci pale yellow.

Posterior margin of head capsule evenly rounded; ocelli rather small, separated from compound eyes by more than own least diameter; postclypeus moderately inflated, Pcl/W, 0.29, Pcl/R_A, 3.00-3.22, posterior margin evenly rounded, median suture distinct. Apical teeth of mandibles short, L_A/L₁, 0.52-0.56, R_A/R₁, 0.75-0.83; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio, L_A/L₁.L_m, 7.70-9.10; points of apical and marginal teeth of right mandible in line, anterior edge of first marginal distinctly longer than that of second. Pilosity of head capsule brown, uneven, no pelt. Meso- and metanota somewhat wider at constriction, M/W, 0.29-0.31. Fore tibia with third apical spur distinct.

Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	0.98-1.01
Ocellus (O _w × O _l)	0.08-0.09 × 0.10-0.13
Ocellus to eye (O-E)	0.07
Postclypeus length (Pcl)	0.28-0.29
Antennal article III	0.04-0.05
Antennal article IV	0.05-0.06
Antennal article V	0.06
Left mandible, apical to first marginal (L _A)	0.08
Left mandible, first to third marginal (L ₁)	0.15-0.16
Left mandible, third marginal to molar (L _m)	0.06-0.07
Right mandible, apical to first marginal (R _A)	0.09
Right mandible, first to second marginal (R ₁)	0.11-0.13



FIGS 106-115. *Astalotermes*, imago head capsules, front and side views. 106, 107, *A. aganus*; 108, 109, *A. hapalus*; 110, 111, *A. ignavus*; 112, 113, *A. mitis*; 114, 115, *A. murcus*.

Right mandible, second marginal to molar (R_m) . . .	0.06-0.07
Mesonotum width (M) . . .	0.29-0.31
Metanotum width (N) . . .	0.29-0.33

Worker. Head capsule pale yellow, pilosity yellow, very sparse and inconspicuous. Postclypeus strongly inflated, Pcl/W , 0.33, Pcl/R_1 , 3.01; apical teeth of mandibles moderately long, L_A/L_1 , 0.72, R_A/R_1 , 1.00; subsidiary tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio, $L_A/L_1.L_m$, 14.41; first marginal tooth of right mandible slightly behind line of apical to second marginal, $R_A/R_1.R_m$, 18.20. Fore tibia scarcely inflated, T_1/T_w , 4.73, third apical spur distinct, about one-third size of other two. Mesenteric junction with proctodeum diagonal, to right of malpighian knot; enteric valve seating lateral in unopened abdomen, prominently two-lobed, connected to second pouch of proctodeum by moderately long neck; membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (one specimen) in millimetres.

Head width (W)	0.88
Fore tibia width (T_w)	0.14
Fore tibia length (T_1)	0.65
Postclypeus length (Pcl)	0.27
Left mandible, apical to first marginal (L_A)	0.09
Left mandible, first to third marginal (L_1) .	0.13
Left mandible, third marginal to molar (L_m)	0.05
Right mandible, apical to first marginal (R_A)	0.09
Right mandible, first to second marginal (R_1)	0.09
Right mandible, second marginal to molar (R_m)	0.06

This species was originally confused with *Alyscotermes kilimandjaricus* (Sjöstedt). It was first recognized in the principal component analysis as an anomalous outlying point at some distance from the cloud represented by the numerous specimens of the latter. This is illustrated in Text-fig. 105, and compared with similar graphs derived from complex ratios. These incorporate most of the variation comprised in the latent roots corresponding to the principal component scores as illustrated, and provide the best discrimination between the two species based on measurements.

A. hapalus has been compared to *A. aganus* and *A. mitis* under the former species heading. *A. ignavus* and *A. murcus* are distinguishable from *A. hapalus* in the imago by their head pilosity, in which very long setae emerge from a shorter pelt, their larger fontanelle, and less inflated postclypeus. The workers of those two species have vestigial third apical spurs on their very slender fore tibiae. Whether or not the abdomen is dehiscent is unknown.

Holotype ♀ imago, paratype ♀ and ♂ imagos and workers from type-colony, KENYA: Ngong Hills (near Nairobi), N.W. end, 16.vi.1953 (*W. A. Sands* collection No. S497) in British Museum (Natural History).

Only the type-series is known. The small colony was found under a loose rock.

Astalotermes ignavus sp. n.

(Text-figs 110, 111, 120, 121 & 138-143; Pl. I, fig. 5)

Imago. Head capsule chestnut-brown, very dark above ocelli; fontanelle nearly as large as ocellus, elongate oval, flat or slightly depressed, brown; medial spot oval, flat, distinctly smaller than fontanelle, chestnut-brown; postclypeus brown, labrum yellow-brown, frontal marks flat, shining, semi-circular, brown; antennae yellow-brown. Pronotum and mesonotum brown, metanotum yellow-brown, transverse, dark sutures weakly present in meso- and metanota; legs, femora pale yellow-brown, tibiae yellow, tarsi pale yellow. Abdominal tergites brown, dorsal stigmata sepia-brown, sternites yellow-brown, paler in middle, ventral stigmata brown, cerci, pale yellow-brown.

Posterior margin of head capsule not quite evenly rounded, slightly undulating immediately behind eyes; ocelli rather small, separated from compound eyes by slightly less than own least diameter; postclypeus weakly inflated, Pcl/W , 0.21, Pcl/R_A , 2.48-2.67, posterior margin obtusely angular, not rounded, median suture distinct. Apical teeth of mandibles short, L_A/L_1 , 0.58-0.59, R_A/R_1 , 0.77-0.84, subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio $L_A/L_1.L_m$, 6.74-6.81; points of apical and marginal tooth of right mandible in line, anterior edge of first marginal distinctly longer than that of second. Pilosity of head capsule brown, very long emergent setae with rough pelt of shorter setae beneath; longest setae reach well beyond outer curve of compound eyes. Meso- and metanota somewhat wider at constriction, M/W , 0.31-0.32. Fore tibia with third apical spur distinct.

Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	1.04-1.11
Ocellus ($O_w \times O_l$)	0.08-0.09 \times 0.11-0.12
Ocellus to eye (O-E)	0.07-0.08
Postclypeus length (Pcl)	0.22-0.23
Antennal article III	0.03-0.04
Antennal article IV	0.04-0.06
Antennal article V	0.03-0.06
Left mandible, apical to first marginal (L_A)	0.09
Left mandible, first to third marginal (L_1)	0.14-0.16
Left mandible, third marginal to molar (L_m)	0.09
Right mandible, apical to first marginal (R_A)	0.08-0.09
Right mandible, first to second marginal (R_1)	0.11
Right mandible, second marginal to molar (R_m)	0.09
Mesonotum width (M)	0.30-0.32
Metanotum width (N)	0.28-0.34

Worker. Head capsule and pilosity pale yellow-brown, the latter long and conspicuous. Postclypeus moderately inflated, Pcl/W , 0.26, Pcl/R_1 , 2.49, apical teeth of mandibles short L_A/L_1 , 0.62, R_A/R_1 , 0.89; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio $L_A/L_1.L_m$, 9.97; apical and marginal teeth of right mandible approximately in line, anterior margin of first marginal slightly longer than that of second, $R_A/R_1.R_m$, 14.20. Fore tibia scarcely inflated, T_1/T_w , 5.21, third apical spur vestigial or absent. Mesenteric junction with proctodeum diagonal, touching malpighian knot on right; enteric valve seating lateral in unopened abdomen, weakly bilobed, connected



FIGS 116-125. *Astalotermes*, imago mandibles. 116, 117, *A. aganus*; 118, 119, *A. hapalus*; 120, 121, *A. ignavus*; 122, 123, *A. mitis*; 124, 125, *A. murcus*.

to second pouch of proctodeum by distinct neck; membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (one specimen) in millimetres.

Head width (W)	0.85
Fore tibia width (T_w)	0.12
Fore tibia length (T_l)	0.63
Postclypeus length (Pcl)	0.22
Left mandible, apical to first marginal (L_A)	0.08
Left mandible, first to third marginal (L_1)	0.13
Left mandible, third marginal to molar (L_m)	0.06
Right mandible, apical to first marginal (R_A)	0.08
Right mandible, first to second marginal (R_1)	0.09
Right mandible, second marginal to molar (R_m)	0.06

This species, with *A. murcus*, is characterized by the very long head setae of the imago which separate these two from the rest of Group II. *A. murcus* differs from *A. ignavus* in having a slightly more evenly rounded head capsule and narrower meso- and metanota. The worker of *A. murcus* has the first marginal tooth of the right mandible somewhat reduced compared with that of *A. ignavus*. The vestigial third spur of the worker fore tibia distinguishes these two species from others of Group II apart from *A. mitis*, but this has a thicker fore tibia, more inflated post-clypeus, and longer apical teeth to the mandibles. *A. irrixosus* which also has a vestigial third tibial spur is much larger, with longer apical teeth, and a very wide notch separating the subsidiary marginal tooth of the left mandible from its molar prominence. Other comparative details are given in the discussion of species already described. One in four specimens of the worker caste of *A. ignavus* shows abdominal dehiscence.

Holotype queen, paratype king and workers from type-colony, CONGO (BRAZZAVILLE): 13 km W. of Brazzaville, 8.vi.1948 (*A. E. Emerson*) in American Museum of Natural History. (Paratype second queen and workers from type-colony, also in BMNH.)

The only known nest-series was collected at the base of a dead stump in an open field.

Astalotermes mitis sp. n.

(Text-figs 112, 113, 122, 123 & 144-149)

Imago. Head capsule sepia-brown, not darker above ocelli; fontanelle small, less than half as long as ocellus, very short oval, somewhat depressed in middle with slight transverse striations, pale yellow-brown; medial spot circular, flat, smaller than fontanelle, sepia-brown; postclypeus brown, labrum yellow-brown; frontal marks flat, crescent-shaped, brown; antennae yellow-brown, pronotum brown, meso- and metanota, yellow-brown; only the latter with transverse dark suture; legs, femora yellow-brown, tibiae paler, tarsi yellow. Abdominal tergites and

dorsal stigmata yellow-brown, sternites and ventral stigmata pale yellow-brown, sternites yellow in middle; cerci yellow.

Posterior margin of head capsule evenly rounded, ocelli medium-sized, separated from compound eyes by slightly less than own least diameter; postclypeus rather weakly inflated, Pcl/W , 0.25, Pcl/R_A , 2.61, posterior margin undulating, not evenly rounded, median suture distinct. Apical teeth of mandibles fairly short, L_A/L_1 , 0.66, R_A/R_1 , 0.86; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 10.55; points of apical and marginal teeth of right mandible in line, anterior edges of marginal teeth almost equal, first slightly longer. Pilosity of head capsule yellow-brown, uneven, no pelt. Meso- and metanota somewhat wider at constriction, M/W , 0.32. Fore tibia with third apical spur distinct.

Measurements (one specimen) in millimetres.

Head width across eyes (W)	1.01
Ocellus ($O_w \times O_l$)	0.08 \times 0.11
Ocellus to eye (O-E)	0.07
Postclypeus length (Pcl)	0.25
Antennal article III	0.04
Antennal article IV	0.04
Antennal article V	0.05
Left mandible, apical to first marginal (L_A)	0.09
Left mandible, first to third marginal (L_1)	0.14
Left mandible, third marginal to molar (L_m)	0.06
Right mandible, apical to first marginal (R_A)	0.10
Right mandible, first to second marginal (R_1)	0.11
Right mandible, second marginal to molar (R_m)	0.06
Mesonotum width (M)	0.33
Metanotum width (N)	0.31

Worker. Head capsule yellow-white, pilosity pale yellow, sparse and fine. Postclypeus rather strongly inflated, Pcl/W , 0.33, Pcl/R_1 , 3.05; apical teeth of mandibles rather long, L_A/L_1 , 0.79, R_A/R_1 , 1.07; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 15.81; first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edges of marginal teeth about equal, $R_A/R_1.R_m$, 21.01. Fore tibia scarcely inflated, T_1/T_w , 4.55, third apical spur vestigial, almost obsolete. Mesenteric junction with proctodeum almost transverse slightly slanted, to right of malpighian knot; enteric valve seating lateral or slightly ventrolateral in unopened abdomen, rather prominently two-lobed, connected to second pouch of proctodeum by long neck, membranous wall of valve beyond cushions without detectable spicules.

Measurements (one specimen) in millimetres:

Head width (W)	0.87
Fore tibia width (T_w)	0.14
Fore tibia length (T_1)	0.63
Postclypeus length (Pcl)	0.28
Left mandible, apical to first marginal (L_A)	0.10
Left mandible, first to third marginal (L_1)	0.13
Left mandible, third marginal to molar (L_m)	0.05

Right mandible, apical to first marginal (R _A)	0·10
Right mandible, first to second marginal (R ₁)	0·09
Right mandible, second marginal to molar (R _m)	0·05

Most of the comparisons between *A. mitis* and other species of Group II have already been made in the preceding descriptions. It is distinguishable from Group III species mainly by the mandible and intestinal characters of the worker caste, and by the vestigial third apical spur of the fore tibia. *A. irrixosus* is larger and has the subsidiary marginal tooth of the left mandible widely separated from the molar prominence. *A. empodius* has narrower meso- and metanota in the imago, and shorter apical teeth to the mandibles. In the worker it is distinguished from *A. mitis* by the almost dorsal, sessile, three-lobed enteric valve seating and the distinct third apical spur of the fore tibiae. The abdomen of the worker of *A. mitis* is definitely dehiscent.

Holotype queen and paratype workers from type-colony, MALAWI: Zomba Mountain, altitude 5,800 ft, 1956 (*A. W. R. MacCrae*) in British Museum (Natural History).

No biological information is available about the single known nest-series.

Astalotermes murcus sp. n.

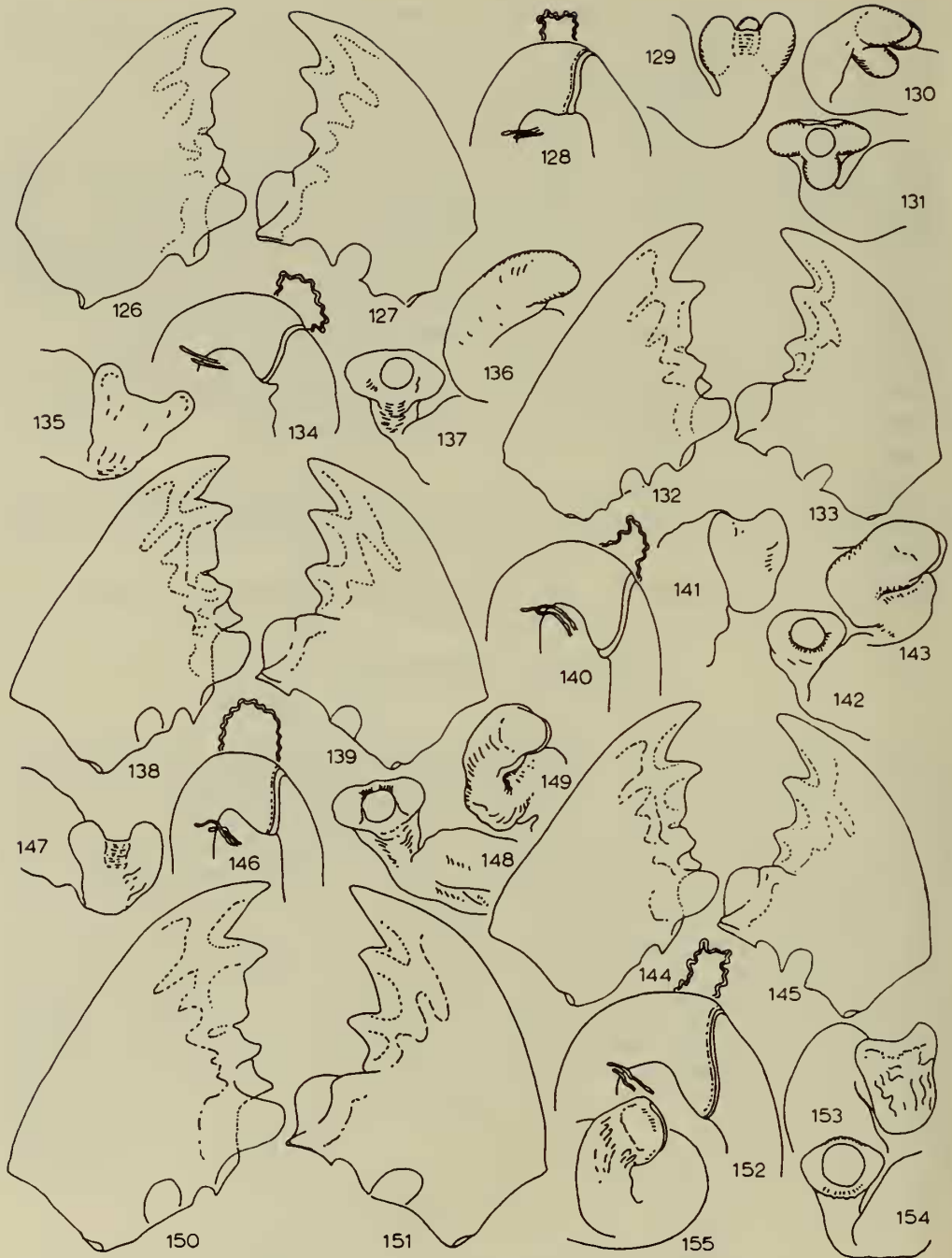
(Text-figs 114, 115, 124, 125 & 150-155)

Imago. Head capsule chestnut-brown, darker above ocelli; fontanelle oval, outline indistinct about half as large as ocellus, flat or slightly depressed, colour as head capsule; medial spot circular, flat, slightly smaller than fontanelle, same colour; postclypeus chestnut-brown, labrum yellow-brown; frontal marks flat, very indistinct crescents, coloured as head; antennae brown. Pronotum chestnut-brown, meso- and metanota brown, transverse sutures weak or absent; legs, femora and tibiae yellow-brown, tarsi pale yellow. Abdominal tergites brown, dorsal stigmata sepia-brown; sternites yellow-brown, yellow in middle, ventral stigmata brown; cerci pale brown.

Posterior margin of head capsule evenly rounded; ocelli rather small, separated from compound eyes by slightly less to slightly more than own least diameter; postclypeus weakly inflated, Pcl/W, 0·19-0·21, Pcl/R_A, 2·33-2·53, posterior margin broadly rounded or slightly angular, median suture very weak. Apical teeth of mandibles short, L_A/L₁, 0·55-0·59, R_A/R₁, 0·83; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio L_A/L₁.L_m, 6·60-6·81; points of apical and marginal teeth of right mandible in line, anterior edge of first marginal distinctly longer than that of second. Pilosity of head capsule brown, very long emergent setae with definite pelt of shorter setae beneath; longest setae reach well beyond outer curve of compound eyes. Meso- and metanota rather narrower at constriction, M/W, 0·26-0·27. Fore tibia with third apical spur distinct.

Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	1·11-1·23
Ocellus (O _w × O _l)	0·08 × 0·10
Ocellus to eye (O-E)	0·07-0·08
Postclypeus length (Pcl)	0·21-0·26
Antennal article III	0·03-0·05



FIGS 126-155. *Astalotermes*, worker mandibles, mesenteric-proctodeal junctions showing attachments of malpighian tubules and positions of malpighian knot, and views of enteric valve seatings. 126-131, *A. aganus*; 132-137, *A. hapalus*; 138-143, *A. ignavus*; 144-149, *A. mitis*; 150-155, *A. murcus*.

Antennal article IV	0.06-0.08
Antennal article V	0.06-0.07
Left mandible, apical to first marginal (L_A)	0.09-0.10
Left mandible, first to third marginal (L_1)	0.16-0.18
Left mandible, third marginal to molar (L_m)	0.08-0.09
Right mandible, apical to first marginal (R_A)	0.09-0.10
Right mandible, first to second marginal (R_1)	0.11-0.13
Right mandible, second marginal to molar (R_m)	0.09
Mesonotum width (M)	0.30-0.32
Metanotum width (N)	0.28-0.34

Worker. Head capsule pale yellow, pilosity yellow, long, numerous and conspicuous. Postclypeus moderately inflated, Pcl/W, 0.30, Pcl/ R_1 , 2.63; apical teeth of mandibles short, L_A/L_1 , 0.64, R_A/R_1 , 0.85; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio $L_A/L_1.L_m$, 7.90; first marginal tooth of right mandible slightly behind line of apical to second marginal, its anterior margin distinctly shorter than that of second, $R_A/R_1.R_m$, 10.46. Fore tibia slender, T_1/T_w , 5.80, third apical spur vestigial. Mesenteric junction with proctodeum diagonal, touching malpighian knot on right; enteric valve seating lateral in unopened abdomen, weakly bilobed, connected to second pouch of proctodeum by long neck; membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (one specimen) in millimetres.

Head width (W)	1.03
Fore tibia width (T_w)	0.14
Fore tibia length (T_1)	0.81
Postclypeus length (Pcl)	0.31
Left mandible, apical to first marginal (L_A)	0.10
Left mandible, first to third marginal (L_1)	0.16
Left mandible, third marginal to molar (L_m)	0.08
Right mandible, apical to first marginal (R_A)	0.10
Right mandible, first to second marginal (R_1)	0.12
Right mandible, second marginal to molar (R_m)	0.08

Comparisons of *A. murcus* with Group II species have been made in the preceding descriptions. Its very close similarity to *A. ignavus* gave rise to some uncertainty as to whether these two should be described separately or considered one species. However, the two records are from over 1,000 miles apart. The differences in the proportions of the mandibles, and the meso- and metanotal constrictions are such as are found between species or even genera that are clearly separated by other characters; they are also found within a single variable species. The decision to split them in the absence of intermediate specimens was taken on the principle that this will cause less confusion in the long run than the converse should either

prove to be wrong. *A. irrixosus* is closer in size to this species than to *A. ignavus*, but it has a more inflated postclypeus and shorter head pilosity in the imago, and the proportions of the worker mandibles are different. *A. empodius* is again distinguished by differing mandibles in both imago and worker, also in the imago by the shorter pilosity and the worker by the very different enteric valve seating. The worker abdomen does not appear to be dehiscent.

Holotype ♀ imago, paratype ♀ and ♂ imagos, and workers from type-colony, ZAMBIA: Ndola, 30.i.1957 (*W. G. H. Coaton*) in National Collection of Isoptera, No. TM 4110, Pretoria.

Other paratype material. ZAMBIA: Kitwe, 23.i.1957 (*W. G. H. Coaton*) in N.C.I. coll. No. TM 3920, Pretoria.

No biological information is available about this species.

Group III

Astalotermes acholus sp. n.

(Text-figs 156-159, 170, 171 & 178-183; Pl. I, fig. 6)

Imago. Head capsule dark sepia-brown, very dark above ocelli; fontanelle subject to pronounced sexual dimorphism, in ♀, large sunken pale brown area approximating in size to compound eye, surface slightly irregular; in ♂, small pitch-black elongate oval, slightly raised, or obsolete, in either case surrounded by very dark sepia-brown flat area larger than ocellus; medial spot circular, flat, minute, sepia-brown; postclypeus pale brown to brown, labrum yellow; frontal marks very indistinct brown crescents, slightly depressed at inner ends; antennae brown. Pronotum sepia-brown, meso- and metanota brown, transverse sutures very weak; legs, femora pale yellow-brown, tibiae yellow, tarsi pale yellow; abdominal tergites and dorsal stigmata sepia-brown, ventral stigmata and sternites brown, the latter paler in middle; cerci pale yellow.

Posterior margin of head capsule slightly undulating, not evenly rounded; ocelli fairly large, separated from compound eyes by less than half own least diameter; postclypeus weakly inflated, Pcl/W, 0.21-0.22, Pcl/R_A, 2.23-2.51, posterior margin bowed, median suture absent. Apical teeth of mandibles short, L_A/L₁, 0.52-0.64, R_A/R₁, 0.64-0.76; subsidiary marginal tooth of left mandible well clear of molar prominence in surface view, complex ratio L_A/L₁.L_m, 6.79-8.09; first marginal tooth of right mandible slightly behind line of apical to second marginal, its anterior margin slightly longer than that of second. Pilosity of head capsule yellow-brown, uneven, no pelt. Meso- and metanota narrow at constriction, M/W, 0.23-0.25. Fore tibia with third apical spur shorter but distinct.

Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	0.85-0.92
Ocellus (O _w × O ₁)	0.08 × 0.11-0.12
Ocellus to eye (O-E)	0.03-0.04
Postclypeus length (Pcl)	0.19-0.20
Antennal article III	0.03-0.04
Antennal article IV	0.04-0.05
Antennal article V	0.04-0.05
Left mandible, apical to first marginal		
(L _A)	0.07-0.09
Left mandible, first to third marginal		
(L ₁)	0.14

Left mandible, third marginal to molar (L _m)	0.08
Right mandible, apical to first marginal (R _A)	0.07-0.09
Right mandible, first to second marginal (R ₁)	0.12
Right mandible, second marginal to molar (R _m)	0.06
Mesonotum width (M)	0.19-0.23
Metanotum width (N)	0.22-0.25

Worker. Head capsule pale yellow, pilosity yellow, fairly sparse. Postclypeus moderately inflated, Pcl/W, 0.27, Pcl/R₁, 1.85; apical teeth of mandibles short, L_A/L₁, 0.51, R_A/R₁, 0.61; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio L_A/L₁.L_m, 10.32; first marginal tooth of right mandible distinctly behind line of apical to second, its anterior margin approximately half length of second, R_A/R₁.R_m, 12.71. Fore tibia weakly inflated, T₁/T_w, 4.02, third apical spur distinct, slightly shorter than other two. Mesenteric junction with proctodeum nearly diagonal, midway through malpighian knot; enteric valve seating ventrolateral in unopened abdomen, weakly three-lobed, third lobe smaller than outer two, sessile on second pouch of proctodeum or with very short neck; membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (one specimen) in millimetres:

Head width (W)	0.70
Fore tibia width (T _w)	0.12
Fore tibia length (T ₁)	0.46
Postclypeus length (Pcl)	0.19
Left mandible, apical to first marginal (L _A)	0.06
Left mandible, first to third marginal (L ₁) .	0.12
Left mandible, third marginal to molar (L _m)	0.05
Right mandible, apical to first marginal (R _A)	0.06
Right mandible, first to second marginal (R ₁)	0.10
Right mandible, second marginal to molar (R _m)	0.05

Although first in alphabetic order in Group III, *A. acholus* is an aberrant species easily distinguished from all others in the imago by the widely sexually dimorphic fontanelle which is extremely conspicuous, particularly in the ♀. In the worker caste the much reduced first marginal tooth characterizes Group III and *A. acholus* is distinguished from *A. brevior*, *A. obstructus* and *A. quietus* in having the enteric valve seating ventrolateral in the unopened abdomen, together with minor features given in the key. The worker abdomen does not appear to be dehiscent.

Holotype ♀ imago, paratype ♀ and ♂ imagos, and workers from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Mbamba (Bas Congo), 6.x.1966 (*C. Nkakala*) in Musée Royal de l'Afrique Centrale, Tervuren. (Paratypes from type-colony, ♀ and ♂ imagos and workers, in British Museum (Natural History) and at University of Lovanium, Kinshasa.)

There is no biological information about the single nest-series.

Astalotermes brevior (Holmgren) comb. et stat. n.

(Text-figs 160-162, 172, 173 & 184-189; Pl. 1, fig. 7)

Mirotermes (*Cubitermes*) *natalensis* form *brevior* Holmgren, 1913 : 357. Syntypes, REPUBLIC OF SOUTH AFRICA: Natal, Zululand, Mkosi (♂ in American Museum of Natural History [examined]; others, sex unknown, in Mus. Göteborg).

Anoplotermes sanctus Silvestri, 1914 : 57. LECTOTYPE ♀, ANGOLA: São Paulo de Loanda (Silvestri Coll., Istituto di Entomologia Agraria, Naples), here designated [examined]. **Syn. n.**

Mirotermes (*Procubitermes*) *mbazwanicus* Fuller, 1925 : 189. LECTOTYPE ♀, REPUBLIC OF SOUTH AFRICA: Natal, Zululand, Mbaswane Swamp (National Collection of Isoptera, Pretoria), here designated [examined]. **Syn. n.**

Mirotermes (?*Procubitermes*) *mfolozii* form *warreni* Fuller, 1925 : 191. LECTOTYPE ♀, REPUBLIC OF SOUTH AFRICA: Natal, Mont aux Sources (National Collection of Isoptera, Pretoria), here designated [examined]. **Syn. n.**

Imago. Head capsule very dark sepia-brown, pitch-black around ocelli and compound eyes; fontanelle variable, from broad oval only slightly smaller than ocelli, brown, and paler than head, to small, elongate oval, coloured as head, and from slightly raised to depressed or with median groove; commonest form depressed elongate oval about half size of ocellus slightly paler than head; medial spot short oval, flat, dark sepia-brown; postclypeus dark sepia-brown, labrum sepia-brown with hyaline tip; frontal marks distinct, semi-circular, depressed, sepia-brown; antennae sepia-brown. Pronotum, meso- and metanota, dark sepia-brown, transverse dark sutures of meso- and metanota very distinct; legs, sepia-brown apart from pale yellow tarsi. Abdominal tergites and sternites sepia-brown, dorsal stigmata darker, sternites paler in mid-line, ventral stigmata slightly darker; cerci brown.

Posterior margin of head capsule undulating, not evenly rounded, ocelli medium-sized, distance from compound eyes varies from just one-half own least diameter up to distinctly more than own least diameter; postclypeus rather weakly to moderately inflated, Pcl/W, 0.23-0.27; Pcl/R_A, 2.74-3.73, posterior margin evenly rounded, median suture usually distinct, always present. Apical teeth of mandibles short, L_A/L₁, 0.41-0.56, R_A/R₁, 0.59-0.79; subsidiary marginal tooth of left mandible just clear of molar prominence on surface view, complex ratio, L_A/L₁.L_m, 6.07-10.00; first marginal tooth of right mandible slightly behind line of apical to second marginal, its anterior margin distinctly shorter than that of second. Pilosity of head capsule generally uneven, no pelt, some specimens slightly more even, sepia-brown. Meso- and metanota less narrow at constriction, M/W, 0.25-0.31. Fore tibia with third apical spur shorter but distinct.

Measurements (30 specimens from 19 localities) in millimetres.

	Range	Mean ± S.D.
Head width across eyes (W)	0.86-1.20	1.043 ± 0.086
Ocellus (O _w × O _l) . . .	0.06-0.10 × 0.10-0.13	0.080 ± 0.009 × 0.109 ± 0.008
Ocellus to eye (O-E) . . .	0.04-0.09	0.066 ± 0.011
Postclypeus length (Pcl) . . .	0.23-0.31	0.262 ± 0.024
Antennal article III . . .	0.02-0.04	0.032 ± 0.006
Antennal article IV . . .	0.03-0.06	0.044 ± 0.007
Antennal article V . . .	0.04-0.06	0.046 ± 0.007
Left mandible, apical to first marginal (L _A) . . .	0.06-0.10	0.081 ± 0.011
Left mandible, first to third marginal (L ₁) . . .	0.13-0.19	0.159 ± 0.016
Left mandible, third marginal to molar (L _m) . . .	0.05-0.08	0.069 ± 0.009



FIGS 156-169. *Astalotermes*, imago head capsules, front and side views. 156-159, *A. acholus* showing sexual dimorphism of fontanelle; 160-162, *A. brevior*, side views show variation of postclypeus; 163, 164, *A. obstructus*; 165-169, *A. quietus*, variation in form.

Right mandible, apical to first marginal (R_A)	0.06-0.10	0.082 ± 0.009
Right mandible, first to second marginal (R_1)	0.09-0.15	0.122 ± 0.013
Right mandible, second marginal to molar (R_m)	0.06-0.09	0.073 ± 0.008
Mesonotum width (M)	0.24-0.35	0.290 ± 0.030
Metanotum width (N)	0.25-0.35	0.302 ± 0.027

Worker. Head capsule yellow-white, pilosity pale yellow, sparse and inconspicuous. Postclypeus moderately to strongly inflated, Pcl/W, 0.29-0.33, Pcl/ R_1 , 2.59-3.08; apical teeth of mandibles short, L_A/L_1 , 0.43-0.54, R_A/R_1 , 0.57-0.76; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 9.38-12.41; first marginal of right mandible distinctly behind line of apical to second, its anterior margin approximately half length of second, $R_A/R_1.R_m$, 11.26-14.10. Fore tibia scarcely inflated, T_1/T_w , 4.32-5.00, third apical spur distinct, one-third to one-half length of other two. Mesenteric junction with proctodeum diagonal or slightly longer, to right of malpighian knot; enteric valve seating dorsolateral in unopened abdomen, weakly two-lobed, sometimes vestige of third lobe, sessile on second pouch of proctodeum; cushions of enteric valve in positions 3 and 4 with a few minute spines on proximal third, membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (12 specimens from 12 localities) in millimetres.

	Range	Mean ± S.D.
Head width (W)	0.75-0.93	0.846 ± 0.045
Fore tibia width (T_w)	0.12-0.14	0.134 ± 0.007
Fore tibia length (T_1)	0.51-0.66	0.622 ± 0.041
Postclypeus length (Pcl)	0.23-0.29	0.262 ± 0.015
Left mandible, apical to first marginal (L_A)	0.06-0.09	0.074 ± 0.009
Left mandible, first to third marginal (L_1)	0.11-0.15	0.133 ± 0.012
Left mandible, third marginal to molar (L_m)	0.04-0.06	0.050 ± 0.004
Right mandible, apical to first marginal (R_A)	0.06-0.08	0.070 ± 0.008
Right mandible, first to second marginal (R_1)	0.08-0.11	0.094 ± 0.010
Right mandible, second marginal to molar (R_m)	0.05-0.07	0.060 ± 0.006

The large number of nest-series of this species available has permitted some study of the variation to be made, as indicated in the description above. This has led to its having been described from different parts of its range under two synonyms. It has been confused with other species in the imago, particularly *Alyscotermes kilimandjaricus* (Sjöstedt) with which it is partly sympatric; however the different proportions of the marginal teeth of the right mandible are diagnostic here. *A. brevior* most closely resembles *A. quietus*, the two being very hard to separate. Such differences as there are, are a matter of degree. In *A. brevior* the imago head pilosity is less even, the postclypeus has a more definite median suture, and the transverse sutures of meso- and metanota are more developed. In general also the ocellus is further from the compound eye, but there is an overlap in this character. In the worker caste there is more distinction in that the reduction of the right first marginal tooth has proceeded further in *A. quietus*, and its enteric valve cushions are completely unarmed. *A. obstructus*, the other Group III species is easily separated, having the ocelli nearly touching the eyes, in the worker by the necked enteric valve, and in both castes by its small size. The abdomen of the worker

caste is very definitely dehiscent, many individuals in most nest-series having ruptured between first and second tergites. Lectotypes of the junior synonyms *A. sanctus* and *A. mbazwanicus* have been selected and labelled and are designated below, together with that of a subspecies, *warreni*, wrongly attributed by Fuller to *A. mfolozii*, which is a synonym of *A. kilimandjaricus* (Sjöstedt).

Type-material. *Mirotermes* (*Cubitermes*) *natalensis* form *brevior* Holmgren, syntype ♂ imago, type-colony, REPUBLIC OF SOUTH AFRICA: Natal, Zululand, Mkosi, 1905 (*I. Trägårdh*), in American Museum of Natural History (other syntypes stated by Holmgren to be in Mus. Göteborg; these have not been examined and therefore no lectotype has been selected). *Anoplotermes sanctus* Silvestri, LECTOTYPE ♀ imago, with paralectotype ♀ and ♂ imagos and workers from type-colony, ANGOLA: Sao Paulo de Loanda, 22.ii.1913 (*F. Silvestri*), in Silvestri Coll., Istituto Entomologia di Agraria, Portici (other paralectotype ♂ imago in AMNH). *Mirotermes* (*Procubitermes*) *mbazwanicus* Fuller, LECTOTYPE ♀ imago, REPUBLIC OF SOUTH AFRICA: Natal, Zululand, Mbazwane swamp, 4.x.1923 (*C. Fuller*), in National Collection of Isoptera, Pretoria (paralectotype, type-colony, in AMNH; other paralectotypes, Durban, 8.ix.1920 (*C. P. Van der Merwe*), in N.C.I., Pretoria and AMNH). *Mirotermes* (? *Procubitermes*) *mfolozii* form *warreni* Fuller, LECTOTYPE ♀ imago, REPUBLIC OF SOUTH AFRICA: Natal, Mont aux Sources, iv.1919 (*E. Warren*), in National Collection of Isoptera, Pretoria.

The specimens named as *Mirotermes* (*Cubitermes*) *natalensis* form *brevior* by Holmgren, and *Mirotermes* (*Procubitermes*) *mbazwanicus* by Fuller were recognized by Dr A. E. Emerson as belonging to *Anoplotermes* sensu lat. It is as a result of his work that they are included here, since in Snyder (1949) they are catalogued under *Procubitermes*. They would have been omitted from this monograph had Dr Emerson not included them in a loan of type-material of *Anoplotermes* from the AMNH.

Other material. REPUBLIC OF SOUTH AFRICA: Cape Province; Port St. Johns, 26.xi.1950, Libode, 22.x.1956, Butterworth, 21.x.1956, and Elliotdale, 20.x.1957 (*W. G. H. Coaton*); Flagstaff (three vials), 12-14.x.1962, Herschel, 8.x, Maclear, Qumbu, Mt Fletcher (three vials), 10.x, Matatiele (six vials) 10-11.x, Mt Currie (two vials), Mt Ayliffe, 12.x, Lusikisiki (five vials), 13-14.x, Tsolo, 15.x, Komgha (seven vials), 21.x, East London (three vials), 22-23.x and Wodehouse (two vials), 5-6.x.1962 (*J. L. Sheasby & G. F. Pretorius*). Orange Free State; Harrismith, 21.xii.1959 (*P. C. Joubert*); Parys, 22.xii.1960 (*H. P. Nieman*); Heilbron (three vials) Kroonstad, 2.x, Lindley (two vials), Vrede, Reitz (three vials) 3.x, Smithfield, 4.x, Harrismith (five vials) 3-5.x, Senekal, Marquand, 6.x, Thaba 'Nchu, De Wetsdorp, Winberg and 7.x, Wepener, 8.x.1962 (*J. L. Sheasby & G. F. Pretorius*); Hoopstad, 25.x.1962 (*W. Mohalo*); Natal, Haviland Rail, xi.1918 (*C. Fuller*); Hlabisa (five vials), 17.xi, Ubombo, 21.xi.1955, Camperdown, 25.x, Lion's River, Newcastle (two vials), 26.x.1956 (*W. G. H. Coaton*); Pietermaritzburg, 5.x.1957 (*D. Fletcher*); Vryheid (two vials), 5.xii, Umvoti, 8.xii, Mapumulo (three vials), Kranskop 10.xii and Bergville, 20.xii.1959 (*P. C. Joubert*); Transvaal, De Wildt, 3.x.1915 and xi.1920, Pretoria, 7.x.1914, 29.x.1915, 21.x.1916 and 27.x.1917 (*C.*

Fuller); Ermelo (two vials), 17.xi.1939, Pretoria, 20.ix and 24.x.1939 and 23.ix.1957, Middelburg (eight vials), 25.x.1955 and (three vials), 28.x.1960, Bronkhorstspuit (two vials), 25.x.1955 and (13 vials), 23-24.ix.1957, Soutpansberg, 9.xii.1956, Carolina, 22.xii.1956 and 26.x.1960, Randfontein (three vials), Potchefstroom and Krugersdorp, 1.x.1956, Volksrust (two vials), 27.x.1956, Heidelberg (four vials), 14.x.1957, Warmbaths (three vials), 25.ix.1957 and 3.x.1960, Groblersdal (three vials), 26.ix.1957, Waterberg, 25.ix.1957 (two vials), 18-19.x.1959, 3.x.1960 and (seven vials), 27.ix.1961, Sibasa (two vials), 24-26.x.1959, Pietersburg (three vials), 5.x.1960, Nelspruit (five vials) 21.x.1960, Marico (two vials), 2.ix.1961 and Rustenburg (seven vials), 26.ix.1961 (*W. G. H. Coaton*); Piet Retief, 5.xi.1947 (*D. V. V. Webb*); Belfast, 27.iv.1936, and Lydenburg, 27.xi.1936 (*J. H. Grobler*); Bronkhorstspuit, 11.xi and Soutpansberg, 31.xii.1960 (*P. C. Joubert*); Lichtenburg, 5.xi.1960 (*H. P. Nieman*), Soutpansberg, 10.x.1960, Rustenburg (three vials), 4.x and Marico (two vials), 5-6.x.1961, Delmas (three vials) and Bethal (two vials), 1.x.1962 (*J. L. Sheasby & G. F. Pretorius*). SWAZILAND: Mbabane, 8.vi.1956 (*J. H. Grobler*); Piggs Peak (two vials), Mbabane, Stegi, Hlatikulu (two vials) and Mankaiama (four vials), 23-26.x.1960 (*W. G. H. Coaton & J. L. Sheasby*). SOUTH WEST AFRICA: Windhoek District, Neudamm-Steinhausen, 2.x.1965, Okavango District, 20 m. from Sakambo-Gowe, 28.iv.1967 (*W. G. H. Coaton*). RHODESIA: Matopos, 22.xi.1965 (*M. G. Bingham*). ZAMBIA: Choma, 14.i.1957 (*W. G. H. Coaton*).

Most of the above material is in the N.C.I., Pretoria, and parts of many nest-series have also been deposited in the BMNH or in the AMNH. A total of 202 nest-series have been examined including the type-material. Little biological information is available but this species has been recorded from the mounds of other genera, and under stones or prone logs. It is the commonest species in south and south-central Africa and extends through south-west Africa to the borders of the Congo, tolerating a fair range of climatic and vegetation types, most of them however relatively dry and open. The species has not been found in rain forest.

Astalotermes obstructus sp. n.

(Text-figs 163, 164, 174, 175 & 196-201)

Imago. Head capsule dark sepia-brown, not darker above ocelli; fontanelle elongate-oval, slightly shorter than ocelli, slightly depressed, brown; medial spot short oval, very small, raised on small bump, sepia-brown; postclypeus sepia-brown, labrum yellow-brown; frontal marks very indistinct, flat, crescent-shaped, sepia-brown; antennae brown. Pronotum sepia-brown, meso- and metanota brown, transverse dark suture only present on metanotum; legs, femora yellow-brown, tibiae paler, tarsi yellow. Abdominal tergites brown, dorsal stigmata paler, sternites and ventral stigmata pale brown, sternites yellow in middle; cerci yellow.

Posterior margin of head capsule not quite evenly rounded, slightly undulating behind eyes; ocelli fairly large, almost touching compound eyes, separated by one-quarter own least diameter or less; postclypeus weakly inflated, Pcl/W , 0.23-0.26, Pcl/R_A , 3.28-3.64, posterior margin obtusely angular, only rounded in middle, median suture distinct posteriorly, absent in front. Apical teeth of mandibles short, L_A/L_1 , 0.50-0.60, R_A/R_1 , 0.63-0.67; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 8.17-10.16; points of apical and marginal teeth of right mandible in line, anterior edges of first and

second marginals approximately equal. Pilosity of head capsule very dense, sepia-brown, uneven, with very strong emergent setae, no pelt. Meso- and metanota less narrow at constriction, M/W, 0.26-0.28. Fore tibia with third apical spur distinct, about half length of others.

Measurements (four specimens from three localities) in millimetres.

	Range	Mean
Head width across eyes (W)	0.76-0.81	0.780
Ocellus ($O_w \times O_l$)	0.08-0.09 \times 0.09-0.11	0.078 \times 0.099
Ocellus to eye (O-E)	0.01-0.02	0.017
Postclypeus length (Pcl)	0.18-0.20	0.193
Antennal article III	0.03-0.04	0.031
Antennal article IV	0.03-0.05	0.039
Antennal article V	—	0.038
Left mandible, apical to first marginal (L_A)	0.05-0.06	0.056
Left mandible, first to third marginal (L_1)	0.10-0.11	0.104
Left mandible, third marginal to molar (L_m)	—	0.060
Right mandible, apical to first marginal (R_A)	0.05-0.06	0.057
Right mandible, first to second marginal (R_1)	0.08-0.09	0.086
Right mandible, second marginal to molar (R_m)	0.05-0.06	0.057
Mesonotum width (M)	0.21-0.24	0.216
Metanotum width (N)	0.21-0.26	0.232

Worker. Head capsule pale yellow-brown, pilosity yellow-brown, sparse but conspicuous owing to colour. Postclypeus moderately inflated, Pcl/W, 0.27-0.28, Pcl/ R_1 , 2.21-2.38; apical teeth of mandibles short, L_A/L_1 , 0.58-0.61, R_A/R_1 , 0.71-0.76; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio, $L_A/L_1.L_m$, 13.90-14.83; first marginal tooth of right mandible distinctly behind line of apical to second, its anterior margin slightly more than half length of second, $R_A/R_1.R_m$, 15.09-17.90. Fore tibia weakly inflated, T_1/T_w , 4.35-4.60, third apical spur small but more than one-quarter length of others, not vestigial. Mesenteric junction with proctodcum slightly longer than diagonal, reaching midway through malpighian knot; enteric valve seating dorso-lateral in unopened abdomen, weakly three-lobed, two outer lobes almost form hood over smaller third, connected to second pouch of proctodeum by short but definite neck; membranous wall of valve beyond cushions with sparse minute spicules.

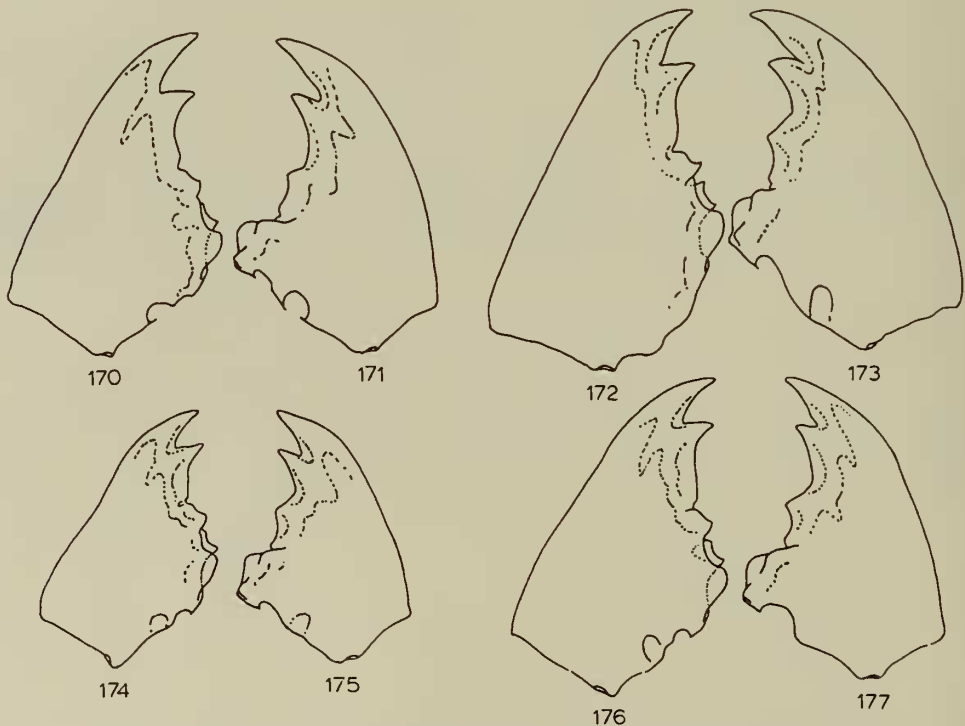
Measurements (three specimens from three localities) in millimetres.

	Range	Mean
Head width (W)	0.64-0.69	0.664
Fore tibia width (T_w)	—	0.108
Fore tibia length (T_1)	0.46-0.50	0.484
Postclypeus length (Pcl)	0.18-0.19	0.183
Left mandible, apical to first marginal (L_A)	—	0.060
Left mandible, first to third marginal (L_1)	—	0.100
Left mandible, third marginal to molar (L_m)	—	0.042
Right mandible, apical to first marginal (R_A)	0.05-0.06	0.059
Right mandible, first to second marginal (R_1)	0.08-0.09	0.080
Right mandible, second marginal to molar (R_m)	0.04-0.05	0.045

A. obstructus is smaller than any other Group III species, and has the first marginal tooth of the right mandible slightly less reduced, in both imago and worker. In this it shows affinities with Groups I and II. In the imago it is separated from all these by the closeness of the ocelli to the compound eyes. In the worker, *A. obstructus* is also distinguished from the rest of Group III by the distinctly necked enteric valve seating, from Group II species by its small size, and from Group I by the shorter right first marginal tooth. The imago of *A. obstructus* was at first confused with that of *Apagotermes stolidus* sp. n., but the meso- and metanota are proportionately wider, the postclypeus longer, and the ocelli are closer to the eyes. The worker of *A. stolidus* is easily recognized by the very characteristic armature of the enteric valve. The abdomen of the worker caste is definitely dehiscent in *A. obstructus*.

Holotype ♀ imago, paratype ♀ and ♂ imagos, and workers from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Epulu R., Camp Putnam, 17.v.1948 (*A. E. Emerson*) in American Museum of Natural History. (Paratypes from type-colony, ♀ and ♂ imagos and workers, in British Museum (Natural History).)

Other paratype material. DEMOCRATIC REPUBLIC OF CONGO: Epulu R., Camp Putnam, 21.v and 22.v.1948, Yangambi, 29.v.1948 (*A. E. Emerson*) (queens, imagos, and workers) in AMNH.



FIGS 170-177. *Astatotermes*, imago mandibles. 170, 171, *A. acholus*; 172, 173, *A. brevior*; 174, 175, *A. obstructus*; 176, 177, *A. quietus*.

The four series of this species known from the depths of the Congo rain forest appear all to have been found in the nests of other genera at the base of forest trees.

Astalotermes quietus (Silvestri) **comb. n.**

(Text-figs 165-169, 176, 177 & 196-201; Pl. I, fig. 8)

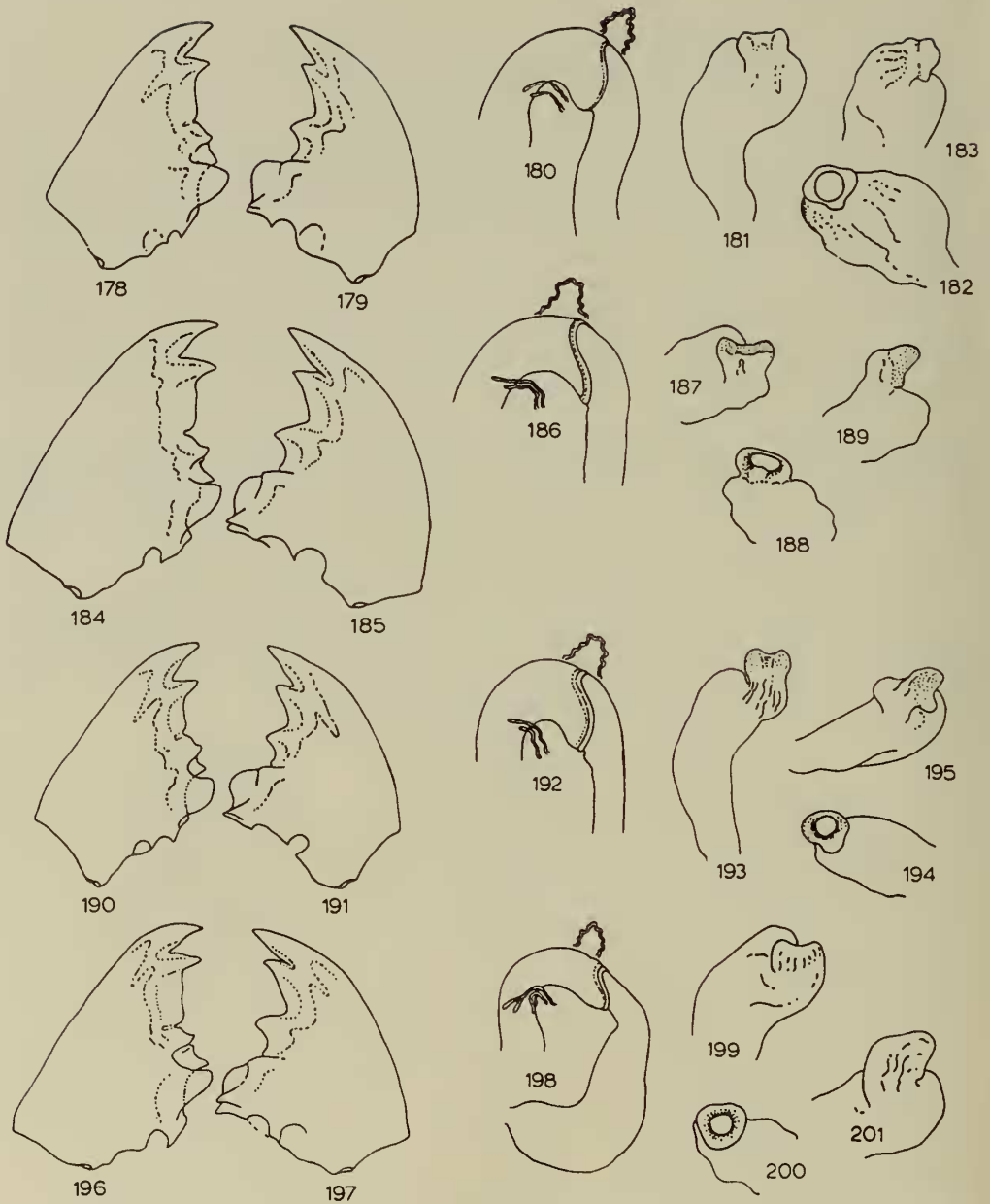
Anoplotermes quietus Silvestri, 1914 : 61. LECTOTYPE ♀, GHANA: Aburi. (Silvestri Coll., Istituto di Entomologia Agraria, Naples), here designated [examined].

Imago. Head capsule dark sepia-brown, very dark above ocelli; fontanelle variable, from broad oval near circular, to elongate oval, from distinctly smaller than ocelli to equal in size, slightly raised, flat or slightly depressed, and from yellow-white, conspicuous, to sepia-brown, scarcely paler than head; commonest form oval, smaller than ocelli, slightly depressed, paler than head; medial spot circular to elongate oval, vestigial to slightly smaller than fontanelle, flat or slightly raised, coloured as head; postclypeus brown to dark sepia-brown, labrum pale brown; antennae brown. Pronotum sepia-brown, meso- and metanota brown, usually with transverse dark sutures; femora brown, tibiae yellow-brown, tarsi yellow. Abdominal tergites and dorsal stigmata sepia-brown, sternites brown, yellow in middle, ventral stigmata brown; cerci yellow-white to pale brown.

Posterior margin of head capsule undulating, rarely approaching evenly rounded; ocelli medium-sized, distance from compound eyes varies from one-quarter, to slightly less than own least diameter; postclypeus very weakly to moderately inflated, Pcl/W, 0.18-0.27, Pcl/R_A, 2.06-3.48, posterior margin evenly rounded in most, sometimes bowed, median suture commonly weak or absent, especially in less inflated forms. Apical teeth of mandibles short, L_A/L_I, 0.42-0.55, R_A/R_I, 0.55-0.74; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio, L_A/L_I.L_m; first marginal tooth of right mandible slightly behind line of apical to second marginal, its anterior margin distinctly shorter than that of second. Pilosity of head capsule brown, short setae an even pelt with longer scattered emergent setae. Meso- and metanota less narrow, somewhat wider at constriction, M/W, 0.26-0.34. Fore tibia with third apical spur shorter but distinct.

Measurements (34 specimens from 23 localities) in millimetres.

	Range	Mean ± S.D.
Head width across eyes (W)	0.82-1.06	0.917 ± 0.061
Ocellus (O _w × O _l) . . .	0.06-0.10 × 0.08-0.14	0.079 ± 0.008 × 0.108 ± 0.013
Ocellus to eye (O-E) . . .	0.02-0.08	0.047 ± 0.013
Postclypeus length (Pcl) . . .	0.16-0.28	0.221 ± 0.027
Antennal article III . . .	0.02-0.05	0.033 ± 0.008
Antennal article IV . . .	0.03-0.06	0.044 ± 0.007
Antennal article V . . .	0.02-0.06	0.043 ± 0.007
Left mandible, apical to first marginal (L _A) . . .	0.06-0.09	0.069 ± 0.008
Left mandible, first to third marginal (L _I) . . .	0.13-0.17	0.147 ± 0.011
Left mandible, third marginal to molar (L _m) . . .	0.06-0.08	0.067 ± 0.006
Right mandible, apical to first marginal (R _A) . . .	0.06-0.09	0.073 ± 0.008
Right mandible, first to second marginal (R _I) . . .	0.10-0.13	0.115 ± 0.008
Right mandible, second marginal to molar (R _m) . . .	0.06-0.08	0.067 ± 0.008
Mesonotum width (M) . . .	0.21-0.34	0.269 ± 0.031
Metanotum width (N) . . .	0.23-0.34	0.275 ± 0.029



FIGS 178-201. *Astalotermes*, worker mandibles, mesenteric-proctodeal junctions showing attachments of malpighian tubules and positions of malpighian knot, and views of enteric valve seatings. 178-183, *A. acholus*; 184-189, *A. brevior*; 190-195, *A. obstructus*; 196-201, *A. quietus*.

Worker. Head capsule yellow-white, pilosity pale yellow, sparse, inconspicuous. Postclypeus weakly to strongly inflated, Pcl/W, 0.24-0.35, Pcl/R₁, 1.89-2.97; apical teeth of mandibles short, L_A/L₁, 0.43-0.54, R_A/R₁, 0.57-0.76; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio, L_A/L₁.L_m, 7.25-11.41; first marginal of right mandible distinctly behind line of apical to second, its anterior margin half length of second or less, R_A/R₁.R_m, 9.94-13.08. Fore tibia scarcely inflated, T₁/T_w, 4.21-5.52, third apical spur distinct, about one-third length of other two. Mesenteric junction with proctodeum diagonal, to right of malpighian knot; enteric valve seating dorso-lateral in unopened abdomen, weakly two-lobed, sessile or second pouch of proctodeum or with very short neck; membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (20 specimens from 20 localities) in millimetres.

	Range	Mean ± S.D.
Head width across eyes (W)	0.71-0.90	0.791 ± 0.055
Fore tibia width (T _w)	0.10-0.14	0.122 ± 0.009
Fore tibia length (T ₁)	0.50-0.66	0.583 ± 0.048
Postclypeus length (Pcl)	0.18-0.29	0.229 ± 0.029
Left mandible, apical to first marginal (L _A)	0.05-0.08	0.064 ± 0.007
Left mandible, first to third marginal (L ₁)	0.11-0.15	0.129 ± 0.008
Left mandible, third marginal to molar (L _m)	0.04-0.06	0.052 ± 0.006
Right mandible, apical to first marginal (R _A)	0.05-0.08	0.064 ± 0.007
Right mandible, first to second marginal (R ₁)	0.09-0.11	0.099 ± 0.008
Right mandible, second marginal to molar (R _m)	0.04-0.06	0.056 ± 0.006

A. quietus is another variable species, which closely resembles *A. brevior* in some of its forms. The differences have already been discussed under that species. The variation in the degree of development of the postclypeus and its median suture is of particular interest. This is most marked in the worker but is reflected in the corresponding imagos. The species has been found in a range of habitats from deep rain forest to small thicket clumps in the savanna zones or even in mounds of other species in open savanna. In the forest specimens the postclypeus tends to be least developed, often lacking a median suture in the imago. The savanna forms have a well developed postclypeus and median suture. The postclypeus is the point at which the cibarial dilator muscles which lift the roof of the buccal cavity are attached. It is therefore probable that the increasing size of the postclypeus in drier conditions accommodates larger muscles better adapted to work the drier soil on which the termites feed. This admittedly speculative interpretation of directional variation appears reasonable in view of the poor flying and hence dispersive powers of these small termites which would tend to perpetuate locally adaptive variants. The same characters of *A. obstructus* that separated it from *A. brevior* also serve to distinguish it from *A. quietus*. Of the other species of *Astalotermes*, *A. benignus* and *A. concilians* are sympatric with *A. quietus*. The small size of *A. benignus* and the vestigial third apical spur of the fore tibia are distinctive; in *A. concilians* the postclypeus is usually more inflated, the meso- and metanota narrower in the imago, and the first marginal tooth of the right mandible is larger. The phenomenon of worker abdominal dehiscence apparently reaches its peak with *A. quietus* in which it is difficult to find an unburst specimen for dissection in most nest-series.

A lectotype has been designated below from the syntype-series of *A. quietus*.

Type-material. *Anoplotermes quietus* Silvestri, LECTOTYPE ♀ imago, paralectotype nymphs and workers from type-colony, GHANA: Aburi, 20.i.1913 (*F. Silvestri*), in Silvestri Coll., Istituto di Entomologia Agraria, Portici, Naples; other paralectotype ♀ imago in AMNH.

Other material. SIERRA LEONE: Kenema, 14.i.1958 (*W. Wilkinson*). GUINEA: Mount Nimba (nine vials), viii, ix.1946 and viii-x.1951 (*M. Lamotte*). IVORY COAST: Banco Forest, 5°22'N., 4°03'W. (three vials), 6.i, 10.i and 10.ii.1962, Bouaflé Forest, 26.ii.1962, Lamto, 5°52'N., 4°46'W., 8.vi.1964 (*E. Ernst*); Banco Forest, 29.vii.1963 (*C. Noirot*); Youhouli, 10 km N. of Dabou (two vials), 16-18.iv.1963 (*P. Bodot*); N'Douci, Lamto, 25.iii, Banco Forest, 21.viii.1950 (*G. Josens*). GHANA: 6 m. N. of Wa on Lawra Road, 19.iii, 52 m. S. of Wa on Sawla Road, 20.iii, 3 m. from Larabanga on Sawla Road, 22.iii, 12 m. from Damongo on Tamale Road, 24.iii, and 7 m. S. of Akumadam on Wenchi-Kumasi Road, 1.iv.1959 (*W. A. Sands*). NIGERIA: Eastern Region; Aba, 27.xii.1956, 47 m. from Enugu on Onitsha Road, 21.i, Onitsha, 5.iv, Port Harcourt 2.v, and 40 m. from Port Harcourt on Owerri Road, 19.vi.1957 (*W. Wilkinson*); Western Region; Olokemeji, near Ibadan, xi.1912 (*F. Silvestri*) (listed in original description, hence paralectotypes not from type-colony), Inst. Ent. Agr., Portici; Northern Region, 18 m. from Kaduna on Zaria Road, 8.xii.1956, Riom, 14.ii, Kwei, 4 m. W. of Jos (two vials), 29.iii, 32 m. from Jos on Kaduna Road, 5.iv, 55 m. from Damaturu on Potiskum Road, 5.vi.1957 and Samaru, near Zaria, 18.v.1959 (*W. A. Sands*). DEMOCRATIC REPUBLIC OF CONGO: St. Gabriel, near Stanleyville, (three vials), 1916 (*H. Kohl*); Stanleyville, 26.v and 3 km from Leopoldville (Kinshasa) on Thysville Road, 16.vi.1948 (*A. E. Emerson*); Yangambi, 30.v.1948 (*W. Emerson*) AMNH; Garamba, 15.iii.1951 (*H. de Saeger*); Kivu District, Wangi (two vials), 2-3.xi.1963 (*E. Ernst*); Mayumbe District, Luki, 19.iv.1965 (*A. Bouillon*); Mondongo District, Lisala, 30.ix.1966 (*J. Ruelle*). RWANDA: Bugesera, 15.xi.1963 (*A. Bouillon*). CONGO (BRAZZAVILLE:): 13 km W. of Brazzaville, 8.vi.1948 (*A. E. Emerson*), AMNH.

A total of 51 nest-series of this species have been examined, and material is in the BMNH except where stated otherwise. More is known of its biology than of any other African member of the group. *A. quietus* has been described by a number of authors as making small 'nests' of a few chambers on twigs or creepers a little above ground level in rain forest. One such was illustrated by Emerson (1928). The 'nest' is sometimes plastered on the side of a tree-trunk. In open savanna this species is commonly found in the mounds of *Cubitermes* spp. The very wide distribution of *A. quietus* from the Western Guinean Savanna to the southern Congo forest is only exceeded by one species of another genus, *Alyscotermes kilimandjaricus* (Sjöstedt).

Other Species

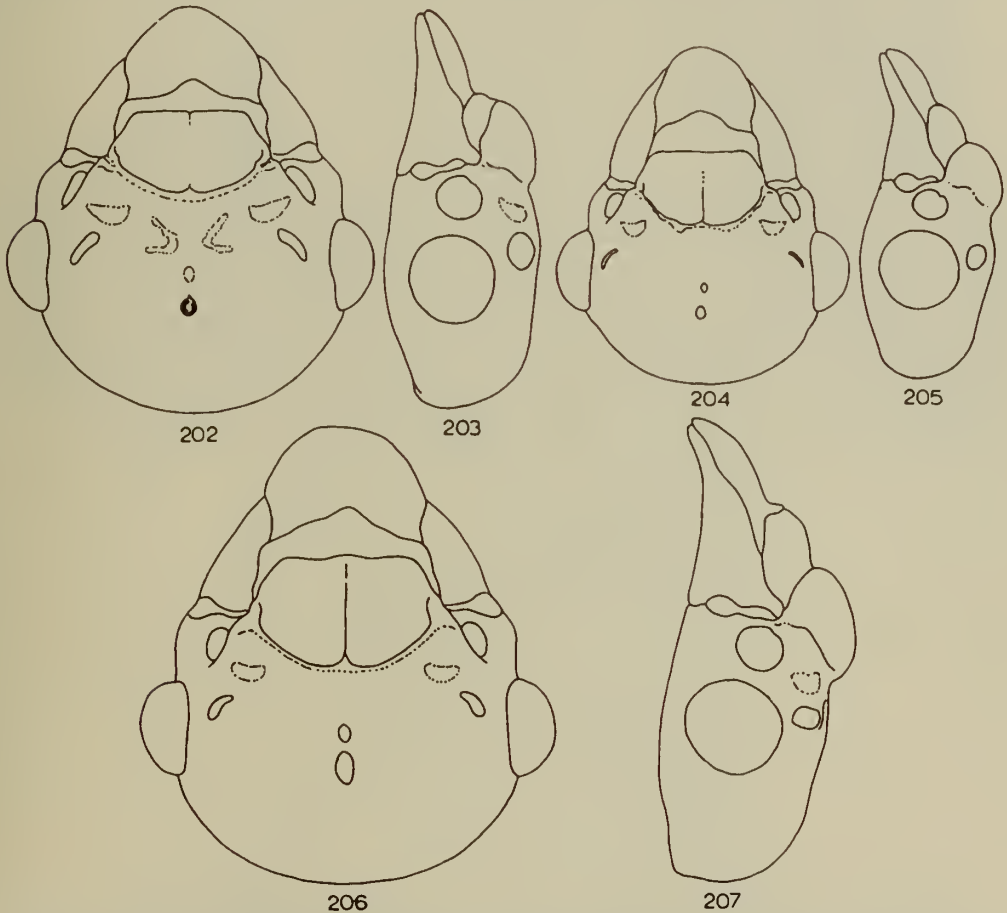
Astalotermes empodius sp. n.

(Text-figs 202, 203, 208, 209 & 214-219; Pl. I, fig. 9)

Imago. Head capsule dark sepia-brown, very dark above ocelli; fontanelle short oval, half size of ocelli or less, depressed, yellow-white to brown; medial spot short oval, very slightly

raised, same size as fontanelle, dark sepia-brown; postclypeus brown to sepia-brown, labrum yellow-brown, frontal marks distinct, semicircular, depressed, brown; antennae brown. Pronotum, meso- and metanota, sepia-brown, transverse dark suture distinct in metanotum only, weak or absent in mesonotum; legs, femora brown, tibiae yellow-brown, tarsi yellow. Abdominal tergites sepia-brown; dorsal stigmata pale brown, sternites brown laterally; paler in middle, ventral stigmata pale brown, cerci pale yellow.

Posterior margin of head capsule evenly rounded; ocelli medium-sized, separated from compound eyes by two-thirds own least diameter or more; postclypeus weakly inflated, $Pc1/W$, 0.22–0.24, $Pc1/R_A$, 2.73–3.15, posterior margin bowed or regularly rounded, median suture usually absent, sometimes weakly present. Apical teeth of mandibles short, L_A/L_1 , 0.46–0.48, R_A/R_1 , 0.62–0.70; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 4.54–5.50; apical and marginal teeth of right mandible in line, anterior edge of first marginal slightly longer than that of second. Pilosity of head capsule dense, brown, uneven, not forming a pelt. Meso- and metanota less narrow at constriction, M/W , 0.26–0.28. Fore tibia with third apical spur distinct, nearly as large as other two.



FIGS 202–207. *Astalotermes*, imago head capsules, front and side views. 202, 203, *A. empodius*; 204, 205, *A. impediens*; 206, 207, *A. irrixosus*.

Measurements (eight specimens from five localities) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	1.13-1.25	1.190 \pm 0.044
Ocellus ($O_w \times O_l$)	0.08-1.10 \times 0.12-0.15	0.095 \pm 0.006 \times 0.133 \pm 0.011
Ocellus to eye (O-E)	0.07-0.10	0.086 \pm 0.009
Postclypeus length (Pcl)	0.25-0.30	0.277 \pm 0.016
Antennal article III	0.02-0.04	0.031 \pm 0.006
Antennal article IV	0.04-0.06	0.047 \pm 0.005
Antennal article V	0.05-0.06	0.049 \pm 0.003
Left mandible, apical to first marginal (L_A)	0.08-0.09	0.088 \pm 0.002
Left mandible, first to third marginal (L_1)	0.18-0.20	0.189 \pm 0.006
Left mandible, third marginal to molar (L_m)	0.09-0.10	0.093 \pm 0.007
Right mandible, apical to first marginal (R_A)	0.09-0.10	0.093 \pm 0.003
Right mandible, first to second marginal (R_1)	0.14-0.15	0.141 \pm 0.005
Right mandible, second marginal to molar (R_m)	0.09-0.10	0.095 \pm 0.006
Mesonotum width (M)	0.25-0.34	0.300 \pm 0.031
Metanotum width (N)	0.28-0.35	0.317 \pm 0.029

Worker. Head capsule yellow-white, pilosity pale yellow, sparse and inconspicuous. Postclypeus moderately inflated, Pcl/W, 0.29-0.30, Pcl/ R_1 , 2.31-2.56; apical teeth of mandibles short, L_A/L_1 , 0.50-0.53, R_A/R_1 , 0.75-0.76; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 9.87-10.00; apical and marginal teeth of right mandible in line, $R_A/R_1.R_m$, 11.89-12.78. Fore tibia scarcely inflated, T_1/T_w , 4.33-4.73, third apical spur small but more than one-quarter other two, not vestigial. Mesenteric junction with proctodeum slightly longer than diagonal, but well to right of malpighian knot; enteric valve seating dorsolateral, almost dorsal, in unopened abdomen, prominently three-lobed, third, inner lobe smaller than outer two, almost completely sessile on second pouch of proctodeum; membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (two specimens from two localities) in millimetres.

Head width (W)	0.88-0.89
Fore tibia width (T_w)	0.14-0.15
Fore tibia length (T_1)	0.65-0.66
Postclypeus length (Pcl)	0.26
Left mandible, apical to first marginal (L_A)	0.08-0.09
Left mandible, first to third marginal (L_1)	0.15-0.16
Left mandible, third marginal to molar (L_m)	0.05
Right mandible, apical to first marginal (R_A)	0.08-0.09
Right mandible, first to second marginal (R_1)	0.10-0.11
Right mandible, second marginal to molar (R_m)	0.06

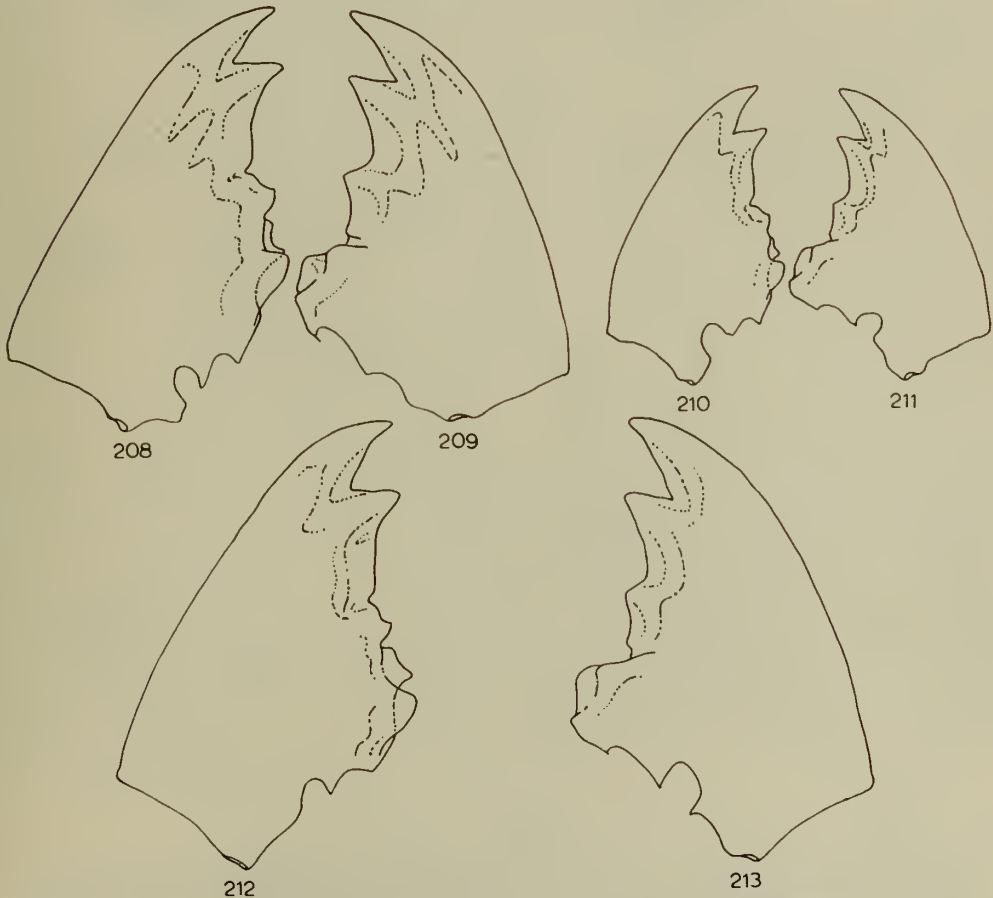
A. empodius will not be confused with any Group I species because it is much larger. Comparisons with Group II species have been made under the headings of its members. In Group III the only species likely to be confused with it is *A. brevior*.

This is distinguishable in the imago by the always distinct median suture of the postclypeus, in both castes by the differing proportions of the mandibular teeth, and further in the worker by the weakly lobed enteric valve seating. It is not known if the abdomen is dehiscent in the worker of *A. empodius*.

Holotype ♀ imago, paratype ♀ and ♂ imagos, and workers, from type-colony, REPUBLIC OF SOUTH AFRICA: Natal, Haviland Rail, xi.1918 (*C. Fuller*, coll. No. F939) in National Collection of Isoptera, Pretoria. (Paratype ♀ and ♂ imagos, and workers from type colony, also in AMNH and BMNH.)

Other paratype material. REPUBLIC OF SOUTH AFRICA: Natal, Estcourt (*G. D. Haviland*, Nos in Fuller collection, F.367, F.936); upper valley or Mkusi River, near Magut, 4.iii.1921 (*G. C. Haines*, No. in Fuller collection F1234); Klipriver, 26.x.1956 (*W. G. H. Coaton*), in N.C.I., Pretoria and AMNH.

The only biological information available for this species is that it has been collected from the mounds of *Cubitermes bilobatus* (Haviland).

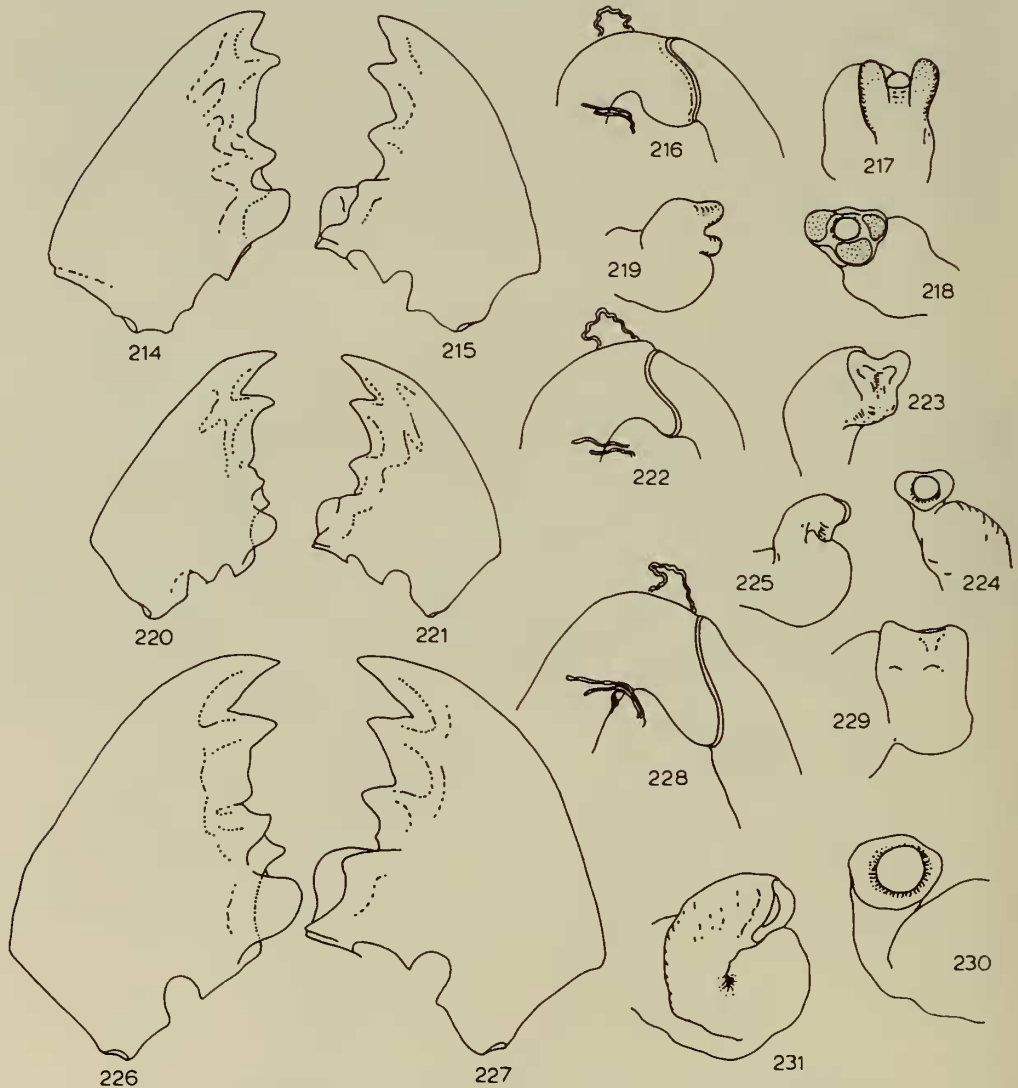


FIGS 208-213. *Astalotermes*, imago mandibles. 208, 209, *A. empodius*; 210, 211, *A. impediens*; 212, 213, *A. irrixosus*.

Astalotermes impediens sp. n.

(Text-figs 204, 205, 210, 211 & 220-225)

Imago. Head capsule brown, not darker above ocelli; fontanelle short oval, less than half size of ocelli, slightly depressed, pale brown; medial spot oval, flat, smaller than fontanelle, brown; postclypeus pale brown, labrum pale yellow; frontal marks small rather indistinct flat pale brown crescents; antennae pale yellow-brown. Pronotum, yellow-brown, meso- and metanota pale yellow-brown, transverse sutures absent on meso-, very weak on metanotum;



FIGS 214-231. *Astalotermes*, worker mandibles, mesenteric-proctodeal junctions showing attachments of malpighian tubules and positions of malpighian knot, and views of enteric valve seatings. 214-219, *A. empodius* (mandibles heavily worn); 220-225, *A. impediens*; 226-231, *A. irrixosus*.

legs, femora yellow-brown, tibiae pale yellow, tarsi yellow-white. Abdominal tergites and dorsal stigmata pale yellow-brown, sternites and ventral stigmata still paler; cerci yellow.

Posterior margin of head capsule evenly rounded; ocelli small, separated from compound eyes by about two-thirds own least diameter; postclypeus moderately inflated, Pcl/W , 0.26, Pcl/R_A , 3.42-3.68, posterior margin somewhat undulating, median suture weak. Apical teeth of mandibles short, L_A/L_1 , 0.41-0.53, R_A/R_1 , 0.62-0.65; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio $L_A/L_1.L_m$, 7.50-8.75; apical and marginal teeth of right mandible in line, anterior edge of first marginal longer than that of second. Pilosity of head capsule pale yellow-brown, uneven, no pelt. Meso- and metanota less narrow at constriction M/W , 0.26-0.27. Fore tibia with third apical spur only slightly smaller than other two.

Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	0.86-0.94
Ocellus ($O_w \times O_l$)	0.06-0.07 \times 0.08-0.09
Ocellus to eye (O-E)	0.04
Postclypeus length (Pcl)	0.23-0.24
Antennal article III	0.04
Antennal article IV	0.04
Antennal article V	0.05
Left mandible, apical to first marginal (L_A)	0.07
Left mandible, first to third marginal (L_1)	0.12-0.14
Left mandible, third marginal to molar (L_m)	0.060-0.07
Right mandible, apical to first marginal (R_A)	0.07
Right mandible, first to second marginal (R_1)	0.10-0.11
Right mandible, second marginal to molar (R_m)	0.05-0.06
Mesonotum width (M)	0.23-0.25
Metanotum width (N)	0.24-0.28

Worker. Head capsule pale yellow, pilosity similarly coloured, fine, silky, inconspicuous but fairly dense. Postclypeus weakly inflated, Pcl/W , 0.25, Pcl/R_1 , 1.91; apical teeth of mandibles short, L_A/L_1 , 0.54, R_A/R_1 , 0.74, subsidiary marginal tooth of left mandible separated from molar prominence by wide notch in surface view, complex ratio $L_A/L_1.L_m$, 12.45; first marginal of right mandible slightly behind line of apical to second marginal, anterior edges of marginal teeth approximately equal, $R_A/R_1.R_m$, 15.91. Fore tibia weakly inflated, T_1/T_w , 4.47, third apical spur small but not vestigial, about one-third other two. Mesenteric junction with proctodeum diagonal, to right of malpighian knot; enteric valve seating lateral in unopened abdomen, two outer lobes well developed, third lobe vestigial, connected to second pouch of proctodeum by fairly long neck; membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (one specimen) in millimetres.

Head width (W)	0.71
Fore tibia width (T_w)	0.12
Fore tibia length (T_1)	0.52
Postclypeus length (Pcl)	0.18
Left mandible, apical to first marginal (L_A)	0.07
Left mandible, first to third marginal (L_1)	0.12

Left mandible, third marginal to molar (L _m)	0.04
Right mandible, apical to first marginal (R _A)	0.07
Right mandible, first to second marginal (R ₁)	0.10
Right mandible, second marginal to molar (R _m)	0.05

This medium-sized species, as stated in the introduction to the genus, resembles the Group I species. It differs from *A. amicus* in the proportionately longer postclypeus and shorter apical teeth of the mandibles. The very different proportions of the mandibles, and in the worker, the gut characters, distinguish *A. comis*. *A. eumenus* has narrower meso- and metanota and longer apical teeth. The other species of Group I are not likely to be sympatric with *A. impediens* and are in any case separable by similar characters. In Group II, *A. hapalus* is rather similar in the imago though larger with wider meso- and metanota, and more inflated postclypeus. In the worker the apical teeth of the mandibles are longer and the postclypeus much more inflated. *A. mitis* is likewise distinguished from *A. impediens* except that the imago postclypeus is not more inflated. *A. murcus* from the same locality as *A. impediens* is much larger with characteristic long head setae. In Group III, *A. brevior* shows resemblances in some forms of the imago, though usually much darker with pronounced transverse sutures on meso- and metanota, and the proportions of mandibular teeth are different. The mandible characters are accentuated in the worker, which also has an almost sessile enteric valve seating. It is not known whether the worker abdomen is dehiscent in *A. impediens*.

Holotype ♀ imago, paratype ♂ imago and worker from type-colony, ZAMBIA: Ndola 30.i.1957 (W. G. H. Coaton) in National Collection of Isoptera, No. TM4111, Pretoria.

No other material of this species is known and there is no information on its biology.

Astalotermes irrixosus sp. n.

(Text-figs 206, 207, 212, 213 & 226-231; Pl. I, fig. 10)

Imago. Head capsule dark chestnut-brown, very dark above ocelli; fontanelle oval, somewhat smaller than ocelli, slightly depressed, chestnut-brown; medial spot oval, flat, equal in size to fontanelle or slightly smaller, colour as head; postclypeus brown, labrum yellow-brown; frontal marks distinct chestnut-brown depressed crescents; antennae brown. Pronotum, meso- and metanota, chestnut-brown, transverse dark sutures present; legs, femora yellow-brown, tibiae paler, tarsi yellow. Abdominal tergites and dorsal stigmata, ventral stigmata and lateral parts of sternites, brown; middle of sternites, and cerci, pale yellow-brown.

Posterior margin of head capsule evenly rounded; ocelli rather small, separated from compound eyes by two-thirds to five-sixths own least diameter; postclypeus moderately inflated, Pcl/W, 0.26-0.27, Pcl/R_A, 2.92-3.17, posterior margin evenly rounded, median suture distinct. Apical teeth of mandibles short, L_A/L₁, 0.52, R_A/R₁, 0.76-0.78; subsidiary marginal tooth of left mandible separated from molar prominence by wide notch in surface view, complex ratio L_A/L₁.L_m, 5.21-5.22; apical and marginal teeth of right mandible in line, anterior edge of first

marginal nearly twice length of second. Pilosity of head capsule chestnut-brown, uneven, no pelt. Meso- and metanota distinctly wider at constriction, M/W, 0.33-0.36. Fore tibia with third apical spur only slightly smaller than other two.

Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	1.24-1.33
Ocellus ($O_w \times O_l$)	0.09 \times 0.12-0.13
Ocellus to eye (O-E)	0.06-0.08
Postclypeus length (Pcl)	0.33-0.36
Antennal article III	0.05
Antennal article IV	0.07-0.08
Antennal article V	0.07
Left mandible, apical to first marginal (L_A)	0.10-0.11
Left mandible, first to third marginal (L_1)	0.19-0.20
Left mandible, third marginal to molar (L_m)	0.10
Right mandible, apical to first marginal (R_A)	0.11
Right mandible, first to second marginal (R_1)	0.14-0.15
Right mandible, second marginal to molar (R_m)	0.10
Mesonotum width (M)	0.41-0.48
Metanotum width (N)	0.43-0.48

Worker. Head capsule orange-yellow, pilosity yellow-brown, sparse but long, coarse and conspicuous. Postclypeus weakly inflated, Pcl/W, 0.25, Pcl/ R_1 , 2.39; apical teeth of mandibles moderately long, L_A/L_1 , 0.73, R_A/R_1 , 1.00; subsidiary marginal tooth of left mandible separated from molar prominence by wide notch in surface view, complex ratio, $L_A/L_1.L_m$, 9.30; first marginal of right mandible very slightly behind line of apical to second marginal, anterior edge of first marginal slightly longer than that of second, $R_A/R_1.R_m$, 13.09. Fore tibia slender, T_1/T_w , 5.96, third apical spur vestigial, one-fifth or less length of other two. Mesenteric junction with proctodeum slightly longer than diagonal, to right of malpighian knot; enteric valve seating dorsolateral in unopened abdomen, very weakly bilobed, connected to second pouch of proctodeum by long neck; membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (one specimen) in millimetres.

Head width (W)	1.08
Fore tibia width (T_w)	0.14
Fore tibia length (T_1)	0.81
Postclypeus length (Pcl)	0.27
Left mandible, apical to first marginal (L_A)	0.12
Left mandible, first to third marginal (L_1)	0.16
Left mandible, third marginal to molar (L_m)	0.08
Right mandible, apical to first marginal (R_A)	0.11
Right mandible, first to second marginal (R_1)	0.11
Right mandible, second marginal to molar (R_m)	0.08

A. irrixosus is the largest species in the genus, although it is approached in size by *A. murcus*, the largest *A. brevior* and *A. empodius*. The characters separating it from *A. murcus* have already been noted; other comparisons are made in the discussions of *A. ignavus* and *A. mitis*. In *A. brevior* the proportions of the mandibles are different in both castes, and the enteric valve seating is sessile. The proportions of the mandibular teeth also distinguish *A. empodius* which in addition has a prominently lobed sessile enteric valve seating. *A. irrixosus* was at first grouped with *Alyscotermes* but this genus has a prominently spined enteric valve, and has the third apical spur well developed on the worker fore tibia, not vestigial. The abdomen of the worker of *A. irrixosus* appears to be dehiscent, but not very markedly so, since the specimens have not burst completely.

Holotype ♀ imago, paratype ♂ imago, workers and nymphs from type-colony, SUDAN: Equatoria Province, Imatong Mountains, 24.vii-5.viii.1939 (*N. A. Weber*), in American Museum of Natural History; paratype ♀ imago and worker in BMNH.

Only the type-series is known, and, apart from the comment on the label 'In separate cells in *Polyrhachis* earth mound, 4500"', there is no information on its biology.

ADYNATOTERMES gen. n.

(Adynatos, Gr., 'weak, without strength')

Type-species: *Mirotermes* (? *Procubitermes*) *moretelae* Fuller, 1925 : 191

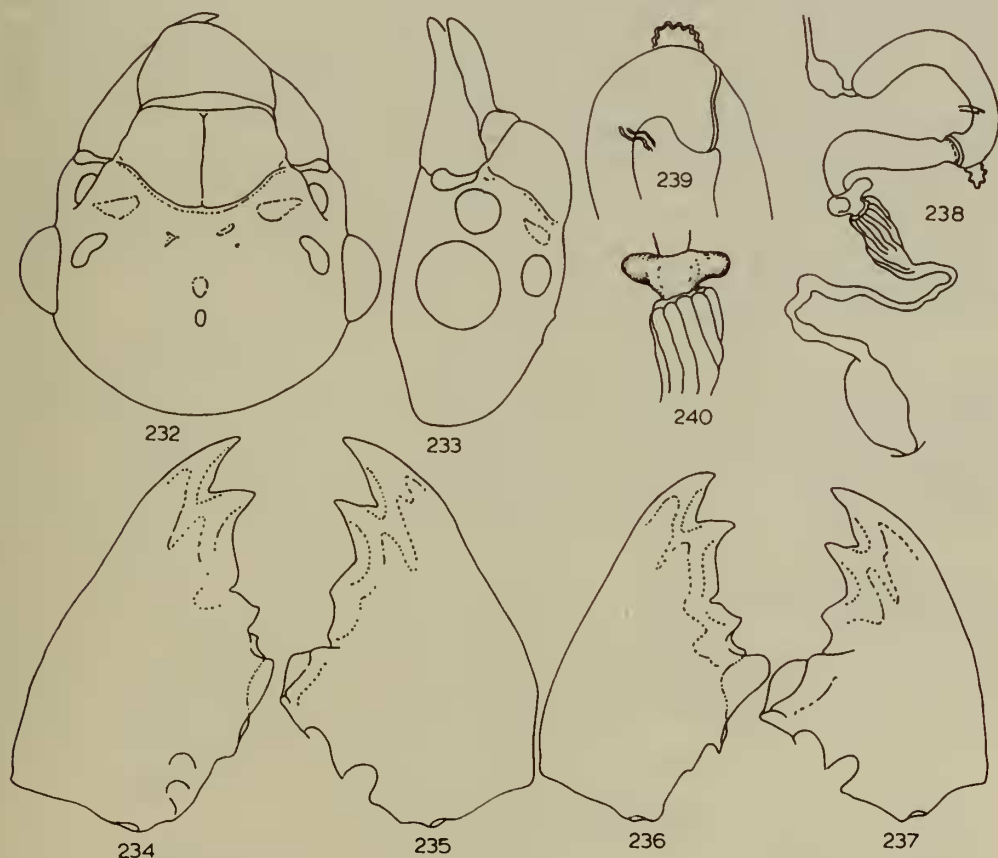
Imago. Large-sized, W, 1.14-1.21. Fore tibia with three apical spurs, third well developed, almost equal to other two. Apical teeth of mandibles short, L_A/L_1 , 0.51-0.57, R_A/R_1 , 0.73-0.87; subsidiary marginal tooth of left mandible with proximal end just level with edge of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 5.98-6.68. Points of apical and marginal teeth of right mandible in line, anterior edges of marginal teeth equal. Meso- and metanota rather narrow at constriction, M/W, 0.24-0.28, transverse dark sutures absent.

Worker. Large, W, 0.85-0.90. Fore tibia weakly swollen. T_1/T_w , 4.13-4.54, with three apical spurs, third about half length of other two. Apical teeth of mandibles short, L_A/L_1 , 0.53-0.60, R_A/R_1 , 0.75-0.82; subsidiary marginal tooth of left mandible with proximal end level with edge of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 10.50-11.86. Points of apical and marginal teeth of right mandible in line, anterior edge of marginal teeth equal, complex ratio $R_A/R_1.R_m$, 11.90-16.50. Mesenteric junction with proctodeum only slightly angled, almost transverse, to right of malpighian knot. Enteric valve seating with two opposite erect lobes, almost diverticula, connected to second pouch of proctodeum by very short neck, lateroventral in position in unopened abdomen; internal cushions of enteric valve without armature, surface faintly reticulated only.

This genus contains a single species, and is separated from *Astalotermes* chiefly on account of the unique development of the enteric valve seating. In the multi-variate similarity analysis, *A. moretelae* is placed close to *Astalotermes empodius*, *A. aganus* and *A. mitis*, both by clustering methods and when plotted as principal co-ordinates. In the latter it is separable from them only by the value of its elements in the fourth and fifth latent vectors. The canonical variates based on the measurements of both imago and worker castes show the same close similarity to *Astalotermes*. Thus it was with some hesitation that *A. moretelae* was consigned

to a further monotypic genus. However, as in *Acidnotermes*, the subsidiary marginal tooth of the left mandible has scarcely emerged from behind the molar prominence. The gut of the worker is shorter than in most *Astalotermes*. In the imago, the fontanelle is usually raised on a distinct bump, and the medial spot is always raised on a second, more prominent bump. These features are found in several other genera, and suggest that although the enteric valve seating is clearly specialized, a number of probably ancestral characteristics have been retained.

Apart from the mandible and fontanelle characters already mentioned, *A. moretelae* differs from *Astalotermes aganus* in the imago in having the ocelli much closer to the eyes; in the worker the two-lobed short-necked enteric valve seating contrasts with the three-lobed long-necked structure of the latter species. The valve seating is also three-lobed in *A. empodius*, which has a shorter postclypeus. This is also true of *A. mitis*, and the worker caste of this species has a long-necked



FIGS 232-240. *Adynatotermes moretelae*. 232, 233, front and side views of imago head capsule; 234, 235, imago mandibles; 236, 237, worker ditto; 238, entire worker intestine; 239, mesenteric-proctodeal junction showing attachment of malpighian tubules and position of malpighian knot; 240, enteric valve seating.

valve seating. *Aganotermes oryctes* sp. n. is sympatric with *A. moretelae* and resembles it slightly in the imago, but the apical teeth of the mandibles are much longer.

Adynatotermes moretelae (Fuller) **comb. n.**

(Text-figs 232-240; Pl. I, fig. 11)

Mirotermes (? *Procubitermes*) *moretelae* Fuller, 1925 : 191. LECTOTYPE ♂, REPUBLIC OF SOUTH AFRICA: Pienaars River. (National Collection of Isoptera, Pretoria) here designated [examined].

Imago. Head capsule brown to sepia-brown, darker above ocelli, dark areas often extending as tapering streaks converging to fontanelle; fontanelle small, short oval, about one-third length of ocellus or less, usually raised on slight bump but sometimes flat or slightly depressed, pale brown, often enclosed by dark area; medial spot short oval, equal to fontanelle or slightly larger, raised on more distinct bump, pale brown; postclypeus yellow to yellow-brown, labrum yellow; frontal marks distinct, flat pale brown crescents; antennae pale yellow-brown. Pronotum, meso- and metanota pale brown to brown; femora pale yellow-brown, tibiae and tarsi yellow. Abdominal tergites, pale brown to brown, sternites pale brown, paler in middle, dorsal and ventra stigmata paler than sclerites; cerci yellow-white.

Posterior margin of head capsule not quite evenly rounded, slightly undulating; ocelli rather large, separated from compound eyes less than half, up to near, own least diameter; postclypeus moderately inflated, Pcl/W, 0.27-0.31, posterior margin bowed, not evenly rounded, median suture distinct. Pilosity of head capsule dense, short, coarse, and uneven in length, not forming a pelt. Other characters in generic diagnosis.

Measurements (13 specimens from eight localities) in millimetres..

	Range	Mean \pm S.D.
Head width across eyes (W)	1.14-1.21	1.165 \pm 0.023
Ocellus ($O_w \times O_l$)	0.10-0.13 \times 0.13-0.16	0.111 \pm 0.007 \times 0.142 \pm 0.009
Ocellus to eye (O-E)	0.04-0.09	0.073 \pm 0.016
Postclypeus length (Pcl)	0.33-0.36	0.343 \pm 0.011
Antennal article III	0.03-0.05	0.038 \pm 0.007
Antennal article IV	0.04-0.07	0.056 \pm 0.008
Antennal article V	0.05-0.06	0.060 \pm 0.004
Left mandible, apical to first marginal (L_A)	0.09-0.10	0.099 \pm 0.003
Left mandible, first to third marginal (L_1)	0.18-0.19	0.184 \pm 0.003
Left mandible, third marginal to molar (L_m)	0.08-0.09	0.086 \pm 0.003
Right mandible, apical to first marginal (R_A)	0.10-0.11	0.106 \pm 0.003
Right mandible, first to second marginal (R_1)	0.13-0.14	0.135 \pm 0.004
Right mandible, second to marginal to molar (R_m)	0.08-0.09	0.085 \pm 0.004
Mesonotum width (M)	0.28-0.33	0.299 \pm 0.016
Metanotum width (N)	0.28-0.33	0.302 \pm 0.014

Worker. Head capsule and pilosity pale yellow, setae fairly numerous but short and inconspicuous. Postclypeus strongly inflated, Pcl/W, 0.31-0.34, Pcl/ R_1 , 2.53-2.77. Mem-

branous wall of enteric valve beyond cushions with sparse minute spicules. Other characters given in generic diagnosis.

Measurements (seven specimens from seven localities) in millimetres.

	Range	Mean \pm S.D.
Head width (W)	0.85-0.90	0.879 \pm 0.019
Fore tibia width (T _w)	0.14-0.16	0.144 \pm 0.008
Fore tibia length (T _l)	0.60-0.65	0.623 \pm 0.015
Postclypeus length (Pcl)	0.28-0.30	0.287 \pm 0.008
Left mandible, apical to first marginal (L _A)	0.08-0.09	0.084 \pm 0.004
Left mandible, first to third marginal (L ₁)	0.14-0.15	0.147 \pm 0.004
Left mandible, third marginal to molar (L _m)	0.05-0.06	0.051 \pm 0.003
Right mandible, apical to first marginal (R _A)	0.08-0.09	0.085 \pm 0.003
Right mandible, first to second marginal (R ₁)	0.10-0.11	0.108 \pm 0.002
Right mandible, second marginal to molar (R _m)	0.05-0.06	0.056 \pm 0.005

The distinguishing features of this species are discussed under the generic heading. It only remains to mention that the abdomen of the worker caste shows no sign of being dehiscent in *A. moretelae*, being without a trace of any line of weakness across the back of the first tergite, and without the slightly humped appearance at this point characteristic of the profile in dehiscent species.

A. moretelae is another of those species names that are included as a result of the observations of Dr A. E. Emerson, since it has been placed hitherto in the genus *Procubitermes* (see also *Adaiphrotermes choanensis*, *Astalotermes brevior*, etc.). A lectotype is designated below from among the syntype series.

Type-material. *Mirotermes* (? *Procubitermes*) *moretelae* Fuller, LECTOTYPE ♂ imago, type-colony, paralectotype ♂ and ♀ imagos, REPUBLIC OF SOUTH AFRICA: Transvaal, The Moretele, Pienaars River, 1.x.1916 (*C. Fuller*, No. F702), in National Collection of Isoptera, Pretoria; other paralectotype in AMNH.

Other material. REPUBLIC OF SOUTH AFRICA: Transvaal, Pretoria (two vials), 1.xi and 6.xi.1945 (*W. G. H. Coaton*); Lichtenburg, (two vials), 1.xi.1960 (*P. C. Joubert & H. P. Nieman*). Orange Free State; Bultfontein, 15.xii and Wes-selsbron, 16.xii.1960 (*H. P. Nieman*); Bultfontein, 28.x.1962 (*G. F. Pretorius*); Hoopstad, 25.x.1963 (*W. Mohale*). Cape Province; Vryburg (five vials), 19-21.i.1960 (*P. C. Joubert*).

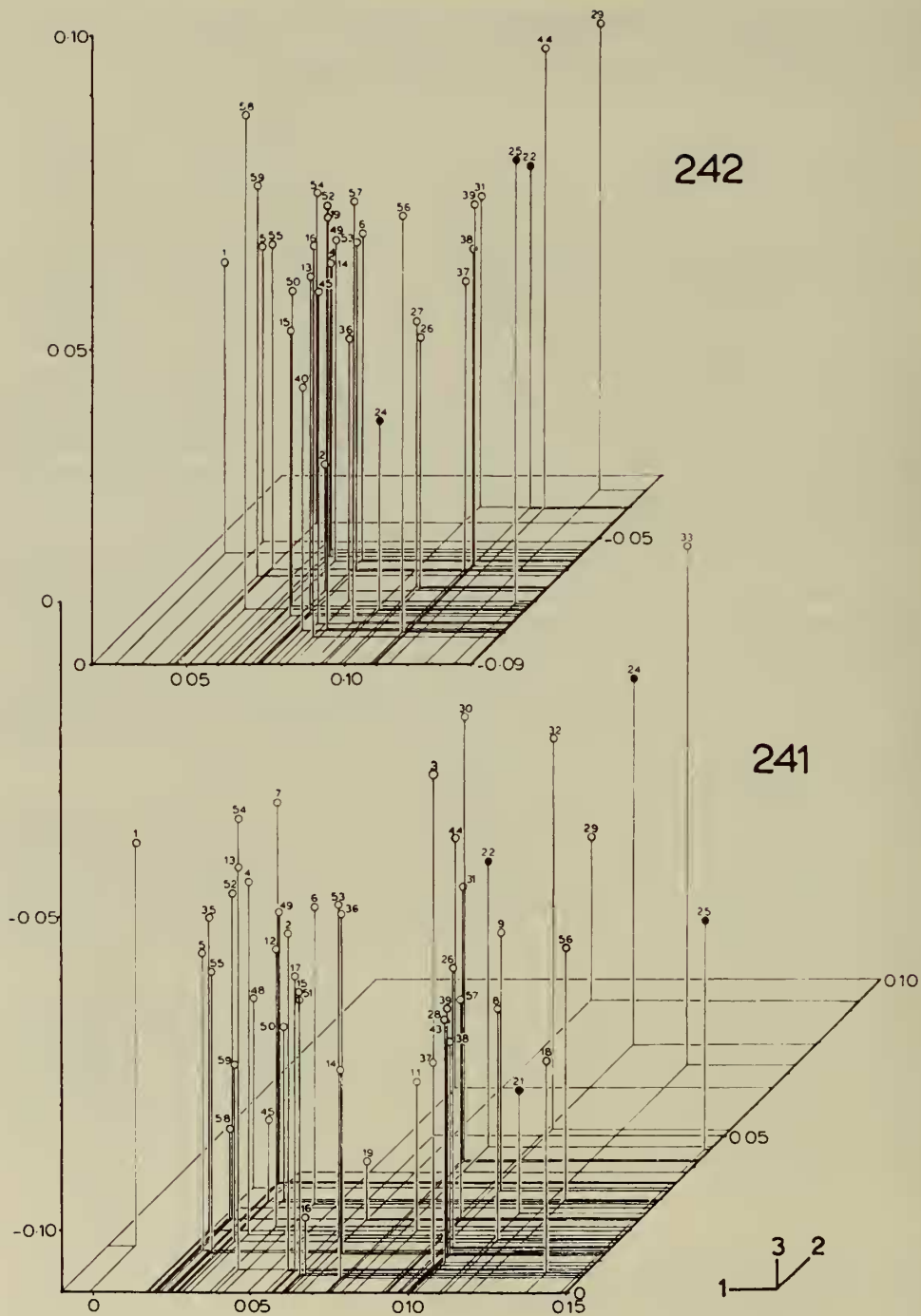
A total of 14 nest-series have been examined. The only biological information is on the type-series which was in the wall of a mound of *Macrotermes natalensis* (Haviland). All the specimens appear to have been collected in the vegetation types 20 or 25 (*Keya et al.*, 1959) inland of the Montane areas (type 6). This contrasts with the smaller number of records of *A. empodius* which was found in type 20 in Natal on the coastal side of the uplands.

ASTRATOTERMES gen. n.

(A—'without, no', stratos, Gr., 'army')

Type-species: *Astratotermes prosenus* sp. n.

Imago. Medium-sized to very large, W, 0.98-1.61. Fore tibia with three apical spurs, third only slightly smaller than other two. Apical teeth of mandibles short to moderately



FIGS 241 & 242. Three-dimensional graphs of canonical variates 1, 2 & 3 showing species of *Astratotermes* as solid spots. 241, imago; 242, worker caste.

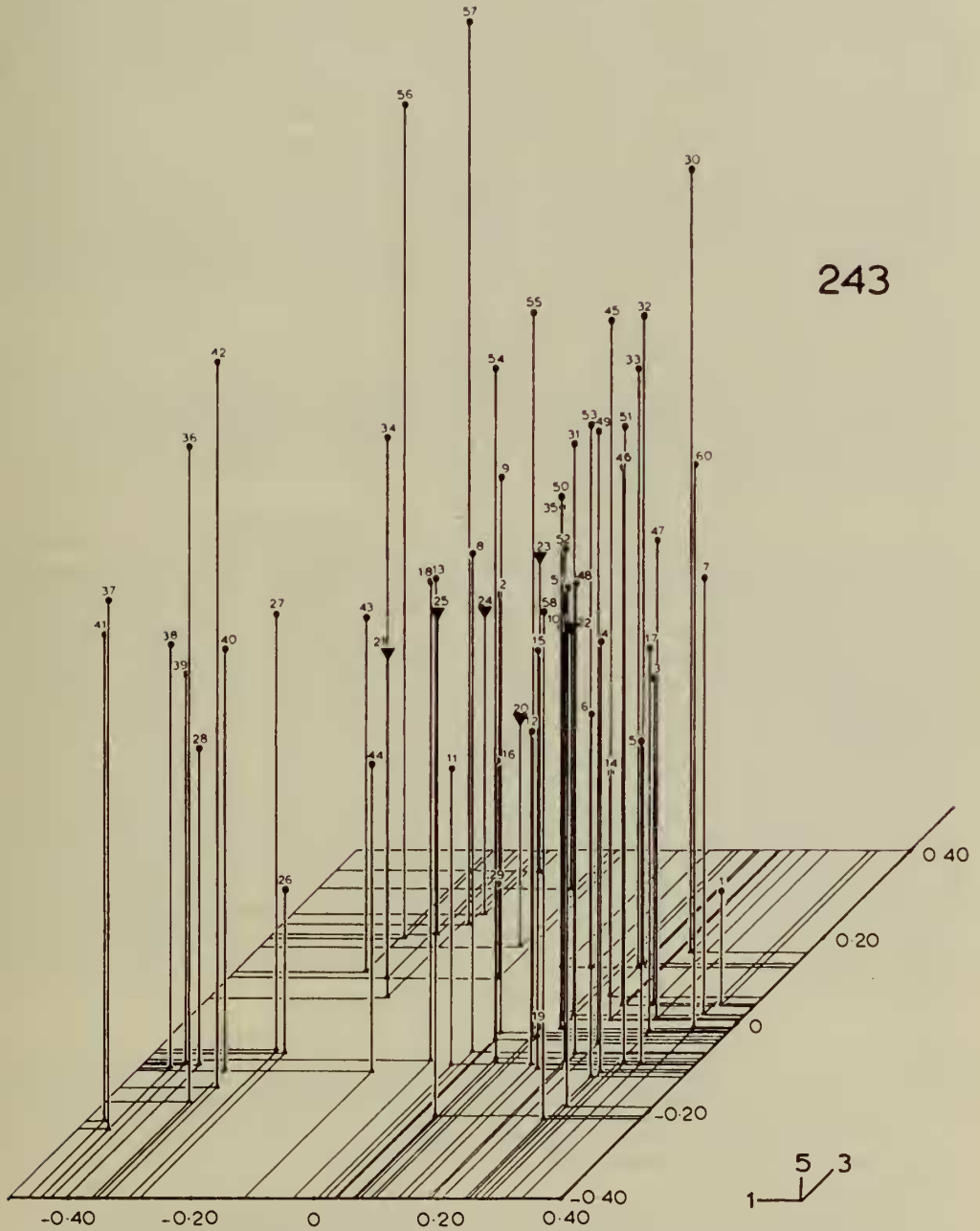


FIG. 243. Three-dimensional graph of principal co-ordinates analysis-plot of eigenvectors 1, 3 & 5 showing species of *Astratotermes* marked by large triangles forming a distinct cluster.

long. L_A/L_1 , 0.46–0.80, R_A/R_1 , 0.58–1.07; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, to widely clear, separated from molar prominence by distinct notch, complex ratio $L_A/L_1.L_m$, 4.70–11.11. Right mandible with points of apical and marginal teeth more or less in line; anterior edge of first marginal distinctly longer than that of second or approximately equal to it. Meso- and metanota from rather narrow to somewhat wider at constriction M/W , 0.24–0.35, transverse dark sutures always present, sometimes weakly developed; complex ratio of mandible and notal measurements, $L_1/M.N$, 0.87–2.36.

Worker. Medium-sized to very large, W , 0.78–1.09. Fore tibia slightly swollen or slender, T_1/T_w , 4.54–7.08, with three apical spurs, third spur distinct, never vestigial. Apical teeth of mandibles short to long, L_A/L_1 , 0.40–0.88, R_A/R_1 , 0.62–1.10; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, to widely clear, separated from molar prominence by deep notch, complex ratio $L_A/L_1.L_m$, 7.47–18.61. Right mandible with apical and marginal teeth in line, or first marginal retracted; anterior edge of first marginal longer than that of second, equal to it, or shorter, complex ratio $R_A/R_1.R_m$, 8.86–21.90. Mesenteric junction with proctodeum varies from diagonal to overlapping by about twice width of mesenteron at insertion of malpighian tubules, proximal end of proctodeum to right of malpighian knot in shorter forms, half-way through it in longer. Enteric valve seating weakly to strongly two- or three-lobed, connected to second pouch of proctodeum by distinct to very long neck, ventral to dorsolateral in position in unopened abdomen; internal cushions of enteric valve scaly, many of scales terminating posteriorly in a single minute spine, none of which protrude through valve opening.

Some species included in this genus appear to be related to some of the species placed in *Astalotermes*, and the only feature in the diagnosis which clearly separates these genera is the presence of small spines in the armature of the enteric valve. There is a considerable spread of variation in other characters such as the imago and worker mandibles, the imago fontanelle, the length of the worker gut as indicated by the position of the enteric valve seating in the unopened abdomen, and in the development of the mixed segment. These suggest that both *Astalotermes* and *Astratotermes* may be artificial assemblages arising from the general similarity of their species in a numerical analysis weighted by the enteric valve structure. However, these two genera are separated from one another by this analysis more widely than some that are homogeneous and easily definable on conventional basis (Text-fig. 243, to be compared with Text-fig. 56). Moreover, attempts to produce genera based on combinations of the characters mentioned above by conventional or purely numerical methods based on measurements alone proved unsuccessful (Text-figs 241, 242). *Astratotermes* is therefore retained, like *Astalotermes*, as a convenient grouping until more ecological and biological information is available.

Astratotermes is distinguishable from *Adaiaphrotermes*, *Aderitotermes* and *Anentotermes* in the worker caste by the short mesenteric overlap with the proctodeum. The workers of *Alyscotermes*, *Anicotermes*, *Apagotermes*, *Ateuchotermes*, *Anaoro-termes* and *Asagarotermes* all possess conspicuous and characteristic spiny enteric valve armature. *Aganotermes* and *Adynatotermes* like *Astalotermes* are devoid of even small spines, *Acholotermes* workers have longer apical teeth to the mandibles, and the postclypeus is less inflated. The remaining genera are smaller. In the imago, recognition of the genera is much more difficult. Of the genera with overlapping size-ranges, *Adaiaphrotermes* lacks a third apical spur on the fore tibia. *Aganotermes* and *Adynatotermes* have the subsidiary marginal tooth of the left

mandible level with the edge of the molar prominence, not clear of it. Their uneven head-pilosity coupled with longer apical teeth to the mandibles serve to separate *Acholotermes* and *Amicotermes*, since in *Astratotermes* with uneven pilosity, the teeth are shorter. *Astratotermes* with an oval fontanelle cannot be separated in the imago by any constant character from *Alyscotermes* or *Astalotermes*. However, it is usually possible to locate the correct genus by trial and error among the specific keys and descriptions when this difficulty arises; under the generic heading of *Alyscotermes* the separate distinctions species by species are given. *Astratotermes* with a circular fontanelle can be distinguished by its sharp clear outline from *Ateuchotermes* or *Anaorotermes*. Finally, *Aderitotermes* has the ocellus closer to the compound eye and shorter apical mandibular teeth.

KEY TO SPECIES

Imagos

- 1 Compound eyes and ocelli proportionately very large and close together, greatest separation between them slightly more than one-third least diameter of ocellus (Text-figs 276-277) ***pacatus*** (p. 120)
- Compound eyes and ocelli smaller and separated by at least two-thirds least diameter of ocellus 2
- 2 Apical teeth of mandibles longer, L_A/L_1 , 0.67-0.80, R_A/R_1 , 0.92-1.07 3
- Apical teeth of mandibles shorter, L_A/L_1 , 0.53-0.59, R_A/R_1 , 0.69-0.76 4
- 3 Larger, W, 1.25-1.61. Fontanelle circular, pale and contrasting with head, flat or slightly depressed. Meso- and metanota wider at constriction, M/W, 0.32-0.35. Pilosity of head an even pelt ***prosenus*** (p. 122)
- Smaller, W, 1.03-1.06. Fontanelle oval, brown, not contrasting with head, slightly raised. Meso- and metanota narrower at constriction. M/W, 0.24-0.28. Pilosity of head uneven, not forming pelt ***hilarus*** (p. 116)
- 4 Smaller, W, 1.09. Postclypeus less prominently inflated, Pcl/W, 0.25. Fontanelle elongate oval, slightly raised. Ocelli separated from compound eyes by about three-quarters own least diameter, $O_w/O-E$, 1.31 ***aneristus*** (p. 110)
- Larger, W, 1.20-1.28. Postclypeus more prominently inflated, Pcl/W, 0.26-0.28. Fontanelle circular or short oval, flat or slightly depressed. Ocelli separated from compound eyes by approximately own least diameter, $O_w/O-E$, 0.90-1.08 5
- 5 Fontanelle large, circular, flat, distinctly paler than head. Apical tooth of left mandible slightly longer, $L_A/L_1.L_m$, 7.53 ***mansuetus*** (p. 118)
- Fontanelle small, oval, slightly depressed, scarcely paler than head. Apical tooth of left mandible shorter, $L_A/L_1.L_m$, 5.63-6.06 ***apocnetus*** (p. 113)

Workers

- 1 Apical teeth of mandibles longer, L_A/L_1 , 0.66-0.88, R_A/R_1 , 0.85-1.10 2
- Apical teeth of mandibles shorter, L_A/L_1 , 0.40-0.58, R_A/R_1 , 0.62-0.75 4
- 2 Apical teeth of mandibles shorter, L_A/L_1 , 0.66, R_A/R_1 , 0.85. Enteric valve seating ventral in unopened abdomen, joined to second pouch of proctodeum by long (length over three times least width) neck. Fore tibia more inflated, T_1/T_w , 4.96 ***mansuetus*** (p. 118)
- Apical teeth of mandibles longer, L_A/L_1 , 0.71-0.88, R_A/R_1 , 1.00-1.10. Enteric valve seating ventrolateral or lateral, with shorter neck (length about twice least width or less). Fore tibia less inflated, T_1/T_w , 5.06-5.75 3
- 3 Larger, W, 1.04-1.09. Postclypeus more inflated, Pcl/R₁, 2.38-2.60. Mesenteric junction with proctodeum diagonal, entirely to right of malpighian knot. Enteric

- valve seating weakly three lobed. Right mandible with anterior edge of first marginal tooth slightly longer than that of second, proportions of teeth, $R_A/R_1.R_m$, 14.49-14.8 **prosenus** (p. 122)
- Smaller, W, 0.79-0.85. Postclypeus less inflated, Pcl/R_1 , 2.00-2.34. Mesenteric overlap with proctodeum, almost twice as long as width of mesenteron at insertion of malpighian tubules, reaching half-way through malpighian knot. Enteric valve seating with two distinct and one smaller lobe. Right mandible with anterior edge of first marginal tooth shorter than that of second, $R_A/R_1.R_m$, 17.3-21.9 **hilarus** (p. 116)
- 4 Fore tibia more inflated, T_1/T_w , 4.54. Apical teeth of mandibles longer, L_A/L_1 , 0.58. Enteric valve seating ventrolateral in unopened abdomen, with three distinct lobes, third only slightly smaller **apocnetus** (p. 113)
- Fore tibia less inflated, T_1/T_w , 5.77-7.08. Apical teeth of mandibles shorter, L_A/L_1 , 0.40-0.49. Enteric valve seating dorsolateral to near dorsal, with two distinct lobes, third vestigial or absent 5
- 5 Mesenteric overlap with proctodeum diagonal, entirely to right of malpighian knot **pacatus** (p. 120)
- Mesenteric overlap with proctodeum twice as long as width of mesenteron at insertion of malpighian tubules, reaching half-way through malpighian knot **aneristus** (p. 110)

Astratotermes aneristus sp. n.

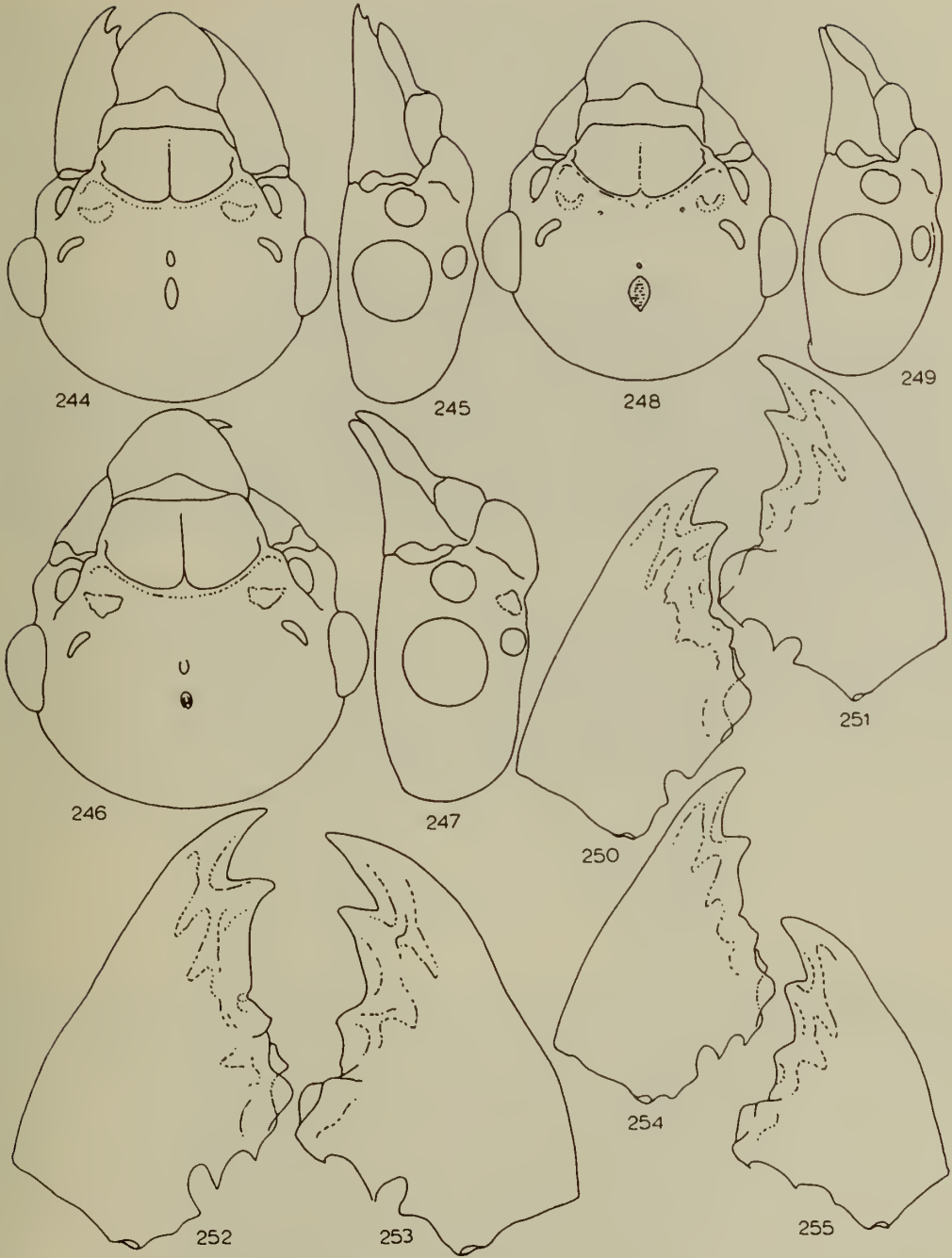
(Text-figs 244, 245, 250, 251 & 256-261; Pl. 2, fig. 1)

Imago. (Queen, colours probably faded.) Head capsule brown, sepia-brown above ocelli; fontanelle only slightly smaller than ocellus, elongate oval, slightly raised, yellow-brown; medial spot oval, about half size of fontanelle, slightly raised, coloured as head; postclypeus yellow-brown, labrum yellow; frontal marks very distinct, slightly depressed yellow-brown crescents; antennae yellow-brown. Pronotum, meso- and metanota yellow-brown, transverse sutures weakly developed; femora pale yellow-brown, tibiae and tarsi yellow. Abdominal tergites yellow-brown with darker dorsal stigmata, ventral stigmata, and sternites pale yellow-brown, paler in middle; cerci yellow.

Posterior margin of head capsule not quite evenly rounded, slightly undulating; ocelli medium sized, separated from compound eyes by three-quarters own least diameter; postclypeus weakly inflated, Pcl/W , 0.25, posterior margin broadly arched, median suture distinct. Apical teeth of mandibles short, L_A/L_1 , 0.53, R_A/R_1 , 0.70; subsidiary marginal tooth of left mandible widely separated from molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 6.00; points of apical and marginal teeth of right mandible approximately in line, anterior edge of first marginal slightly shorter than that of second. Meso- and metanota moderately wide at constriction, M/W , 0.30. Pilosity of head capsule, yellow-brown, short setae rather even, almost forming a pelt, obscured by numerous uneven emergent setae.

Measurements (one specimen) in millimetres.

Head width across eyes (W)	1.09
Ocellus ($O_w \times O_l$)	0.08 \times 0.13
Ocellus to eye (O-E)	0.06
Postclypeus length (Pcl)	0.27
Antennal article III	0.05
Antennal article IV	0.07
Antennal article V	0.07
Left mandible, apical to first marginal (L_A)	0.09
Left mandible, first to third marginal (L_1)	0.17



FIGS 244-255. *Astratotermes*, imago head capsules, front and side views, and imago mandibles. 244, 245 & 250, 251, *A. aneristus*; 246, 247 & 252, 253, *A. apocnetus*; 248, 249 & 254, 255, *A. hilarus*.

Left mandible, third marginal to molar (L_m)	0.09
Right mandible, apical to first marginal (R_A)	0.09
Right mandible, first to second marginal (R_1)	0.13
Right mandible, second marginal to molar (R_m)	0.08
Mesonotum width (M)	0.33
Metanotum width (N)	0.33

Worker. Head-capsule and pilosity, pale yellow, setae very sparse and scattered, inconspicuous. Postclypeus moderately inflated, Pcl/W, 0.27, Pcl/ R_1 , 2.02. Apical teeth of mandibles short, L_A/L_1 , 0.48, R_A/R_1 , 0.67; subsidiary marginal tooth of left mandible separated from molar prominence by wide deep notch in surface view, complex ratio $L_A/L_1.L_m$, 7.70; apical and marginal teeth of right mandible approximately in line, anterior edges of first and second marginals equal, $R_A/R_1.R_m$, 11.96. Fore tibia very slender, T_1/T_w , 6.02, third apical spur distinct, half length of other two. Mesenteric overlap at junction with proctodeum about twice as long as width of mesenteron at insertion of malpighian tubules, proctodeum reaching half-way through malpighian knot; enteric valve seating slightly dorso-lateral in unopened abdomen, with two distinct lateral lobes and vestigial third, inner lobe, connected to second pouch of proctodeum by pronounced neck; membranous wall of valve beyond cushions with very sparse minute spicules.

Measurements (one specimen) in millimetres.

Head width (W)	0.85
Fore tibia width (T_w)	0.11
Fore tibia length (T_1)	0.66
Postclypeus length (Pcl)	0.23
Left mandible, apical to first marginal (L_A)	0.07
Left mandible, first to third marginal (L_1) .	0.15
Left mandible, third marginal to molar (L_m)	0.06
Right mandible, apical to first marginal (R_A)	0.08
Right mandible, first to second marginal (R_1)	0.11
Right mandible, second marginal to molar (R_m)	0.06

The slight tendency in *A. aneristus* for the first marginal tooth of the right mandible to be reduced, and the beginnings of a mixed segment in the gut suggest weak affinities with *Anenteotermes*. Similar tendencies are also found in other genera such as *Astalotermes* and *Acholotermes*, but the species concerned, *A. brevior* and *A. epius*, both have differently proportioned mandibular teeth from *A. aneristus*. Of the other species of *Astratotermes*, *A. apocnetus* is distinguishable in the imago by its smaller fontanelle, smaller ocelli further from the eyes, and more inflated postclypeus; the worker has a short mesenteric-proctodeal junction, to the right of the malpighian knot, and a prominently three-lobed enteric valve seating ventro-lateral in position in the unopened abdomen. *A. hilarus* has longer apical teeth to the mandibles. *A. mansuetus* is larger, with more inflated postclypeus, a large circular fontanelle, and in the worker, a ventral enteric valve seating with three

prominent lobes. The large eyes and ocelli of *A. pacatus* are distinctive, and the subsidiary tooth of the left mandible is only just clear of the molar plate. The type-species, *A. prosenus*, is very large, with a circular pale fontanelle and longer apical mandibular teeth. The worker abdomen of *A. aneristus* is not dehiscent.

Holotype ♀ imago (queen) and six paratype workers from type-colony only, ZAMBIA: Kitwe, 23.i.1957 (*W. G. H. Coaton*) in National Collection of Isoptera, No. TM.3927, Pretoria.

Only the type nest-series is known, and there is no information on its biology.

Astratotermes apocnetus sp. n.

(Text-figs 246, 247, 252, 253 & 262-267)

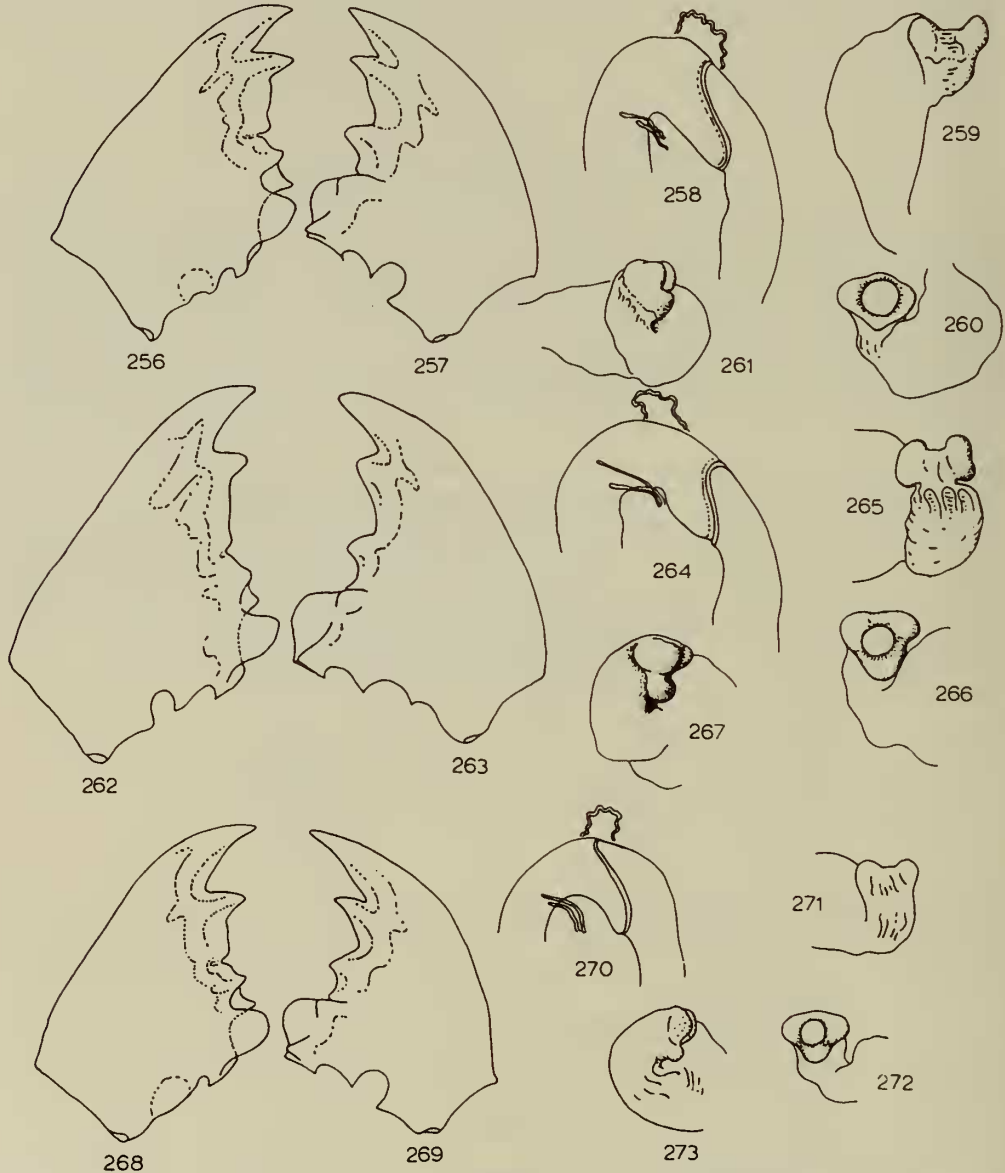
Imago. Head capsule very dark chestnut-brown, pitch-black above ocelli; fontanelle less than half size of ocellus, somewhat irregular oval, slightly depressed or ridged in middle, dark chestnut-brown, medial spot same size as fontanelle, slightly raised or nearly flat, short oval, coloured as head; postclypeus sepia-brown, labrum yellow-brown, frontal marks distinct, somewhat depressed, semicircular, dark chestnut-brown; antennae brown. Pronotum dark sepia-brown, meso- and metanota chestnut-brown, transverse dark sutures distinct; legs, femora sepia-brown, tibiae yellow-brown, tarsi yellow. Abdominal tergites and dorsal stigmata sepia-brown, ventral stigmata and lateral parts of sternites brown, middle of sternites paler; cerci yellow.

Posterior margin of head capsule evenly rounded; ocelli rather small, separated from compound eyes by approximately own least diameter; postclypeus moderately inflated, Pcl/W, 0.27-0.28, posterior margin evenly rounded, median suture very distinct. Apical teeth of mandibles short, L_A/L_1 , 0.49-0.66, R_A/R_1 , 0.69-0.70; subsidiary marginal tooth of left mandible widely separated from molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 5.63-6.06; point of first marginal tooth of right mandible slightly behind line from apical to second marginal, anterior edges of marginal teeth approximately equal in length. Meso- and metanota moderately wide at constriction, M/W, 0.30-0.31. Pilosity of head capsule brown, uneven, no pelt.

Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	1.20-1.28
Ocellus ($O_w \times O_l$)	0.08-0.09 × 0.10-0.11
Ocellus to eye (O-E)	0.08-0.09
Postclypeus length (Pcl)	0.33-0.36
Antennal article III	0.05-0.06
Antennal article IV	0.06
Antennal article V	0.06-0.07
Left mandible, apical to first marginal (L_A)	0.12
Left mandible, first to third marginal (L_1)	0.21-0.23
Left mandible, third marginal to molar (L_m)	0.09-0.10
Right mandible, apical to first marginal (R_A)	0.12-0.13
Right mandible, first to second marginal (R_1)	0.17-0.18
Right mandible, second marginal to molar (R_m)	0.09
Mesonotum width (M)	0.37-0.39
Metanotum width (N)	0.36-0.41

Worker. Head capsule pale yellow, pilosity fairly numerous, rather short, yellow. Post-clypeus weakly inflated, Pcl/W , 0.24, Pcl/R_1 , 1.73. Apical teeth of mandibles short, L_A/L_1 , 0.58, R_A/R_1 , 0.75; subsidiary marginal tooth of left mandibles separated from molar prominence by wide deep notch in surface view, complex ratio $L_A/L_1.L_m$, 9.10; first marginal tooth of right mandible distinctly behind line of apical to first marginal, anterior edge of first marginal shorter



FIGS 256-273. *Astratotermes*, worker mandibles, mesenteric-proctodeal junctions showing attachments of malpighian tubules and positions of malpighian knot, and views of enteric valve seatings. 256-261, *A. aneristus*; 262-267, *A. apocnetus* (mandibles rather worn); 268-273, *A. hilarus*.

than that of second, $R_A/R_1.R_m$, 11.91. Fore tibia scarcely inflated, T_1/T_w , 4.54, third apical spur about half length of other two but pale, inconspicuous. Mesenteric overlap with proctodeum diagonal or slightly less, to right of malpighian knot; enteric valve seating ventrolateral in unopened abdomen, distinctly three-lobed, third inner lobe slightly smaller, connected to second pouch of proctodeum by distinct neck; membranous wall of valve beyond cushions without detectable spicules.

Measurements (one specimen) in millimetres.

Head width (W)	1.00
Fore tibia width (T_w)	0.16
Fore tibia length (T_1)	0.74
Postclypeus length (Pcl)	0.24
Left mandible, apical to first marginal (L_A)	0.10
Left mandible, first to third marginal (L_1) .	0.18
Left mandible, third marginal to molar (L_m)	0.06
Right mandible, apical to first marginal (R_A)	0.10
Right mandible, first to second marginal (R_1)	0.14
Right mandible, second marginal to molar (R_m)	0.06

The features distinguishing *A. apocnetus* from *A. aneristus* have been given under that species. *A. hilarus* has a larger fontanelle, shorter postclypeus and longer apical teeth to the mandibles in the imago. The worker also has longer apical teeth and a longer mesenteric proctodeal overlap. In *A. mansuetus* the fontanelle is large, circular and flat, and the mandibles slightly different in proportions in the imago; the worker has longer apical teeth, and the subsidiary marginal of the left mandible is only just clear of the molar prominence. *A. pacatus* is distinguishable by the large eyes and ocelli of the imago, and by the slender fore tibia, two-lobed enteric valve-seat, and differently proportioned mandibles of the worker. *A. prosenus* is larger, with longer apical teeth in both castes. The imago also has a pale fontanelle and even pilosity, and the worker a slender fore tibia. Outside *Astratotermes*, *Astalotermes irrixosus* was at first thought to be the same species. However, in the imago, the proportions of mandibular teeth are slightly different, the ocellus is closer to the eye and the meso- and metanota are proportionately slightly wider. In the worker, apart from the unarmed enteric valve, the fore tibia has a vestigial third spur and is distinctly thinner, the mesenteric overlap is longer, and the enteric valve seat dorsolateral. The abdomen of the worker caste is dehiscent in *A. apocnetus*.

Holotype ♀ imago, paratype ♀ and ♂ imagos, and workers from type-colony, KENYA: Kisumu, 13.viii.1940 (*E. E. Haviland* coll. No. T3) in American Museum of Natural History. (Paratype ♀ and ♂ imago and worker from type-colony also in BMNH.)

Only the type-series is known, and there is no information on its biology.

Astratotermes hilarus sp. n.

(Text-figs 248, 249, 254, 255 & 268-273; Pl. 2, fig. 2)

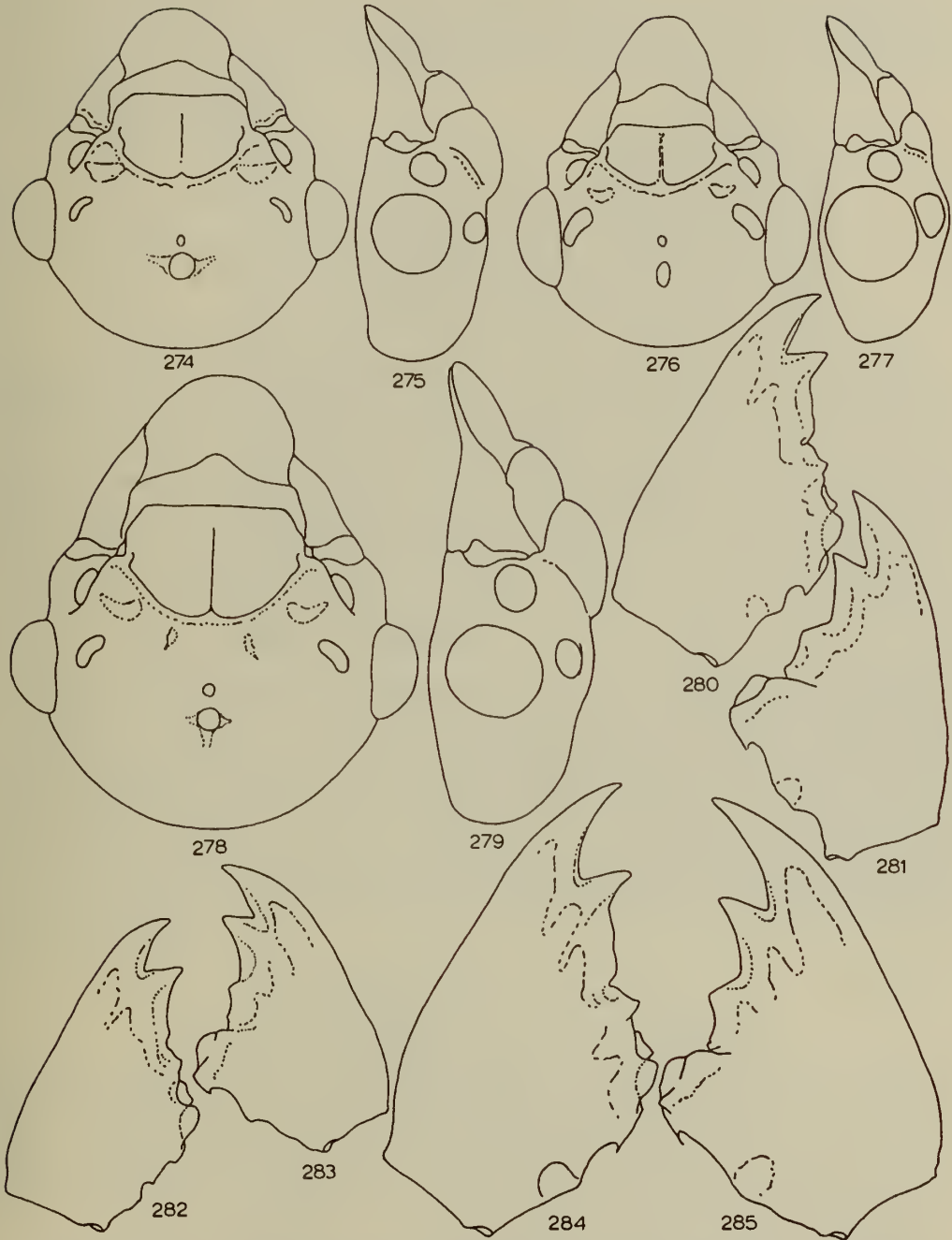
Imago. (Queens and kings only available, colours may be faded.) Head capsule chestnut-brown, darker above ocelli; fontanelle nearly same size as ocellus, slightly raised, short oval, brown; medial spot very small, slightly raised, circular, coloured as head; postclypeus brown, labrum yellow; frontal marks indistinct flat brown crescents; antennae brown. Pronotum, meso- and metanota brown, transverse dark sutures very distinct; legs, femora pale brown, tibia yellow-brown, tarsi yellow. Abdominal tergites and dorsal stigmata brown, ventral stigmata and sternites pale brown laterally, yellow in middle; cerci pale yellow-brown.

Posterior margin of head capsule evenly rounded; ocelli medium-sized, separated from compound eyes by two-thirds up to own least diameter, postclypeus weakly inflated, Pcl/W, 0.21-0.24, posterior margin arched, not evenly rounded, median suture weakly developed. Apical teeth of mandibles moderately long, L_A/L_1 , 0.67-0.80, R_A/R_1 , 0.95-1.07; subsidiary marginal tooth of left mandible widely separated from molar prominence in surface view, $L_A/L_1 L_m$, 10.07-11.11; point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edges of marginal teeth approximately equal. Meso- and metanota rather narrow at constriction, M/W, 0.24-0.28. Pilosity of head capsule brown, uneven, no pelt.

Measurements (five specimens from three nest-series) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	1.03-1.06	1.041 \pm 0.016
Ocellus ($O_w \times O_l$)	0.07-0.10 \times 0.10-0.12	0.084 \pm 0.010 \times 0.113 \pm 0.009
Ocellus to eye (O-E)	0.06-0.09	0.067 \pm 0.010
Postclypeus length (Pcl)	0.23-0.25	0.240 \pm 0.011
Antennal article III	0.04-0.05	0.047 \pm 0.003
Antennal article IV	0.05-0.06	0.051 \pm 0.004
Antennal article V	0.05-0.06	0.056 \pm 0.004
Left mandible, apical to first marginal (L_A)	0.11-0.12	0.115 \pm 0.004
Left mandible, first to third marginal (L_1)	0.15-0.17	0.159 \pm 0.007
Left mandible, third marginal to molar (L_m)	0.06-0.07	0.068 \pm 0.004
Right mandible, apical to first marginal (R_A)	0.11-0.12	0.115 \pm 0.003
Right mandible, first to second marginal (R_1)	0.11-0.12	0.113 \pm 0.003
Right mandible, second marginal to molar (R_m)	0.07-0.08	0.074 \pm 0.002
Mesonotum width (M)	0.25-0.30	0.269 \pm 0.019
Metanotum width (N)	0.26-0.30	0.275 \pm 0.018

Worker. Head capsule pale yellow, pilosity rather sparse but strong and conspicuous, yellow. Postclypeus moderately inflated, Pcl/W, 0.25-0.29, Pcl/ R_1 , 2.00-2.34. Apical teeth of mandibles long, L_A/L_1 , 0.80-0.88, R_A/R_1 , 1.04-1.10; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, $L_A/L_1 L_m$, 16.42-18.61; first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal shorter than that of second, $R_A/R_1 R_m$, 17.30-21.90. Fore tibia slender, T_1/T_w , 5.06-5.75, third apical spur distinct, about half length of other two. Mesenteric overlap with proctodeum about twice as long as width of mesenteron at insertion of malpighian tubules, proctodeum reaching half-way through malpighian knot; enteric valve seating ventrolateral in unopened abdomen, rather weakly three-lobed, third lobe smaller, connected to second pouch



FIGS 274-285. *Astratotermes*, imago head capsules, front and side views, and imago mandibles. 274, 275 & 280, 281, *A. mansuetus* ♂; 276, 277 & 282, 283, *A. pacatus*; 278, 279 & 284, 285, *A. prosenus*.

of proctodeum by distinct neck. Membranous wall of valve beyond cushions without detectable spicules.

Measurements (three specimens from three nest-series) in millimetres.

	Range	Mean
Head width (W)	0.79-0.85	0.812
Fore tibia width (T_w)	0.10-0.11	0.107
Fore tibia length (T_1)	0.57-0.58	0.574
Postclypeus length (Pcl)	0.20-0.23	0.219
Left mandible, apical to first marginal (L_A)	0.10-0.11	0.105
Left mandible, first to third marginal (L_1)	—	0.126
Left mandible, third marginal to molar (L_m)	0.04-0.05	0.047
Right mandible, apical to first marginal (R_A)	0.01-0.11	0.105
Right mandible, first to second marginal (R_1)	—	0.099
Right mandible, second marginal to molar (R_m)	0.05-0.06	0.055

Comparisons of *A. hilarus* with *A. aneristus* and *A. apocnetus* have already been made under those species-headings. In *A. mansuetus* the imago is distinguished by its large fontanelle, more inflated postclypeus, and shorter mandibular apical teeth. The latter feature also applies to the worker in which the anterior edges of right first and second marginals are approximately equal. The enteric valve seating has a very long neck in this species. In *A. pacatus* the large eyes and ocelli characterize the imago which, like the worker, has shorter apical teeth. The enteric valve seating is two-lobed and dorsal in *A. pacatus* workers. *A. prosenus* is again easily recognized by its large size, pale fontanelle, even pilosity, and, in the worker, its short mesenteric overlap with the proctodeum. The worker abdomen appears dehiscent in *A. hilarus*.

Holotype ♀ imago (queen), paratype ♂ (king) and workers from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Katanga, Keyberg, 21.iv.1948 (*A. E. Emerson*) in American Museum of Natural History.

Other paratype material: DEMOCRATIC REPUBLIC OF CONGO: Katanga, Keyberg (two vials), 21 & 25.iv.1948 (*A. E. Emerson*), in AMNH. (One paratype queen and worker also in BMNH.)

The three known nest-series, all from the same locality, were recorded from the mounds of *Cubitermes* sp. and *Trinervitermes* sp. in savanna woodland.

Astratotermes mansuetus sp. n.

(Text-figs 274, 275, 280, 281 & 286-291; Pl. 2, fig. 4)

Imago. Head capsule sepia-brown, darker above ocelli; fontanelle slightly smaller than ocellus, circular, flat, pale yellow-brown; medial spot circular, less than half size of fontanelle, slightly raised, brown; postclypeus brown, labrum yellow; frontal marks distinct, flat, semi-circular, brown; antennae very pale yellow-brown. Pronotum, meso- and metanota brown, transverse dark sutures present but not distinct; legs, femora pale yellow-brown, tibiae paler, tarsi yellow-white. Abdominal tergites pale brown, dorsal stigmata paler, sternites yellow-brown, ventral stigmata pale; cerci yellow-white.

Posterior margin of head capsule not quite evenly rounded, slightly undulating behind eyes; ocelli medium-sized, separated from compound eyes by about own least diameter; postclypeus moderately inflated, Pcl/W, 0.26, posterior margin evenly rounded, median suture present. Apical teeth of mandibles short, L_A/L_1 , 0.59, R_A/R_1 , 0.76; subsidiary marginal tooth of left

mandible separated from molar prominence by distinct notch in surface view, complex ratio, $L_A/L_1.L_m$, 7.53; points of apical and marginal teeth of right mandible approximately in line, anterior edges of first and second marginals nearly equal. Meso- and metanota moderately wide at constriction, M/W , 0.30. Pilosity of head capsule pale brown, rather even, almost a pelt with longer emergent setae.

Measurements (one specimen) in millimetres.

Head width across eyes (W)	1.21
Ocellus ($O_w \times O_l$)	0.09×0.13
Ocellus to eye (O-E)	0.09
Postclypeus length (Pcl)	0.31
Antennal article III	0.05
Antennal article IV	0.06
Antennal article V	0.06
Left mandible, apical to first marginal (L_A)	0.11
Left mandible, first to third marginal (L_1)	0.18
Left mandible, third marginal to molar (L_m)	0.08
Right mandible, apical to first marginal (R_A)	0.10
Right mandible, first to second marginal (R_1)	0.14
Right mandible, second marginal to molar (R_m)	0.08
Mesonotum width (M)	0.37
Metanotum width (N)	0.38

Worker. Head capsule yellow-white, pilosity very sparse, inconspicuous pale yellow; postclypeus moderately inflated, Pcl/W , 0.30, Pcl/R_1 , 2.45. Apical teeth of mandibles fairly short, L_A/L_1 , 0.66, R_A/R_1 , 0.85; subsidiary marginal tooth of left mandibles just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 9.95; point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edges of first and second marginals approximately equal, $R_A/R_1.R_m$, 12.85. Fore tibia scarcely swollen, T_1/T_w , 4.96, third apical spur small but clearly present, not vestigial. Mesenteric overlap at junction with proctodeum diagonal, to right of malpighian knot; enteric valve seating ventral in unopened abdomen, with three pronounced lobes, third lobe slightly smaller, attached to second pouch of proctodeum by very long neck; membranous wall of valve beyond cushions with minute spicules.

Measurements (one specimen) in millimetres.

Head width (W)	0.95
Fore tibia width (T_w)	0.15
Fore tibia length (T_1)	0.73
Postclypeus length (Pcl)	0.29
Left mandible, apical to first marginal (L_A)	0.10
Left mandible, first to third marginal (L_1)	0.15
Left mandible, third marginal to molar (L_m)	0.07
Right mandible, apical to first marginal (R_A)	0.10
Right mandible, first to second marginal (R_1)	0.12
Right mandible, second marginal to molar (R_m)	0.07

Comparisons have already been made between *A. mansuetus* and *A. aneristus*, *A. apocnetus* and *A. hilarus*. The large eyes and ocelli that characterize *A. pacatus* in the imago have also been mentioned. In the worker caste this species differs from *A. mansuetus* in having a very slender fore tibia, shorter mandibular apical teeth, and a two-lobed dorsal enteric valve seating. *A. prosenus* has longer apical teeth in both castes; the worker caste also has a more slender fore tibia, and a shorter-necked enteric valve seating. In the few specimens of the worker caste of *A. mansuetus* that are available there is no sign of abdominal dehiscence.

Holotype ♂ imago, paratype ♂ and workers from type-colony, KENYA: 4 miles from Kaptagat on Eldoret Road, 13.v.1954 (*R. M. C. Williams* Coll. No. RW43) in British Museum (Natural History).

The single type-nest-series was found in a mound of *Cubitermes* sp.

Astratotermes pacatus (Silvestri) comb. n.

(Text-figs 276, 277, 282, 283 & 292-297; Pl. 2, fig. 3)

Anoplotermes pacatus Silvestri, 1914 : 54. LECTOTYPE ♀, GUINEA: Kindia. (Silvestri Coll., Istituto di Entomologia Agraria, Naples) here designated [examined].

Anoplotermes sedatus Silvestri, 1914 : 55. LECTOTYPE ♀, CONGO (BRAZZAVILLE): Brazzaville. (Silvestri Coll., Istituto di Entomologia Agraria, Naples) here designated [examined].

Syn. n.

Imago. Head capsule sepia-brown, not darker above ocelli; fontanelle medium-sized, but less than half as large as ocelli, oval, flat, pale brown; medial spot very small, almost obsolete broad oval, brown; postclypeus brown, labrum yellow; frontal marks small, flat, semicircular, brown, antennae brown. Pronotum sepia-brown, meso- and metanota brown, transverse sutures present, legs, femora yellow-brown, tibiae paler, tarsi yellow. Abdominal tergites sepia-brown, dorsal stigmata pale yellow-brown, ventral stigmata similar, sternites pale brown laterally, paler middle, cerci yellow.

Posterior margin of head capsule widely arched, slightly undulating; ocelli and compound eyes large, separated by up to one-third least diameter of ocellus; postclypeus weakly inflated, Pcl/W, 0.19-0.23, posterior margin arched or sinuate, not evenly rounded, median suture present, not always complete. Apical teeth of mandibles short, L_A/L_1 , 0.46-0.60, R_A/R_1 , 0.58-0.78; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 4.70-8.11, points of apical and marginal teeth of right mandible approximately in line, anterior edge of first marginal nearly twice length of second. Meso- and metanota moderately wide at constriction, M/W, 0.29-0.32. Pilosity of head capsule close and even, forming a pelt with longer emergent setae.

Measurements (seven specimens from four localities) in millimetres.

	Range	Mean ± S.D.
Head width across eyes (W)	0.98-1.21	1.062 ± 0.090
Ocellus ($O_w \times O_l$)	0.11-0.14 × 0.14-0.19	0.118 ± 0.013 × 0.154 ± 0.015
Ocellus to eye (O-E)	0.02-0.04	0.030 ± 0.006
Postclypeus length (Pcl)	0.21-0.23	0.226 ± 0.007
Antennal article III	0.04-0.07	0.050 ± 0.011
Antennal article IV	0.05-0.08	0.060 ± 0.011
Antennal article V	0.05-0.08	0.059 ± 0.010
Left mandible, apical to first marginal (L_A)	0.08-0.09	0.085 ± 0.003

Left mandible, first to third marginal (L_1)	0.14-0.19	0.160 ± 0.021
Left mandible, third marginal to molar (L_m)	0.07-0.10	0.080 ± 0.011
Right mandible, apical to first marginal (R_A)	0.08-0.09	0.085 ± 0.005
Right mandible, first to second marginal (R_1)	0.11-0.15	0.125 ± 0.016
Right mandible, second marginal to molar (R_m)	0.06-0.09	0.077 ± 0.011
Mesonotum width (M)	0.29-0.39	0.321 ± 0.039
Metanotum width (N)	0.30-0.40	0.341 ± 0.032

Worker. Head capsule yellow-white, pilosity sparse, yellow. Postclypeus weakly to moderately inflated, Pcl/W , 0.22-0.29, Pcl/R_1 , 1.65-2.38. Apical teeth of mandibles short, L_A/L_1 , 0.40-0.49, R_A/R_1 , 0.62-0.71; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 7.47-9.56; apical and marginal teeth of right mandible approximately in line, anterior edges of first and second marginals equal, $R_A/R_1.R_m$, 8.86-13.92. Fore tibia very slender, T_1/T_w , 5.77-7.08, third apical spur distinct. Mesenteric overlap at junction with proctodeum diagonal, to right of malpighian knot; enteric valve seating dorsal on right hand side of unopened abdomen, distinctly two-lobed, connected to second pouch of proctodeum by short neck; membranous wall of valve beyond cushions with minute spicules.

Measurements (three specimens from three localities) in millimetres.

	Range	Mean
Head width (W)	0.78-0.93	0.850
Fore tibia width (T_w)	0.09-0.12	0.110
Fore tibia length (T_1)	0.56-0.85	0.704
Postclypeus length (Pcl)	0.19-0.25	0.215
Left marginal, apical to first marginal (L_A)	0.07-0.08	0.073
Left mandible, first to third marginal (L_1)	0.14-0.19	0.161
Left mandible, third marginal to molar (L_m)	0.05-0.06	0.055
Right mandible, apical to first marginal (R_A)	0.07-0.08	0.073
Right mandible, first to second marginal (R_1)	0.11-0.13	0.113
Right mandible, second marginal to molar (R_m)	0.05-0.07	0.057

The characters that distinguish *A. pacatus* from *A. aneristus*, *A. apocnetus*, *A. hilarus* and *A. mansuetus* have already been given under those species. There only remains the type-species of the genus, *A. prosenus*, to be compared. This is larger than *A. pacatus*, with proportionately smaller eyes and ocelli, longer mandibular apical teeth, and differently proportioned marginals on the right. It also has a circular pale fontanelle. The worker of *A. prosenus* also has longer apical teeth, more inflated postclypeus, and a slightly thicker fore tibia. The abdomen of the worker caste is dehiscent in *A. pacatus*.

Lectotypes have been designated from the existing syntype material of *A. pacatus* (Silvestri) and *A. sedatus* (Silvestri) as indicated below.

Type-material. *Anoplotermes pacatus* Silvestri, LECTOTYPE ♀ imago, paralectotype ♂ imagos and workers from type-colony, GUINEA: Kindia, 10°N., 12°45'W., 21.viii.1912 (*F. Silvestri*), in Silvestri Coll., Istituto di Entomologia Agraria, Portici, Naples. *Anoplotermes sedatus* Silvestri, LECTOTYPE ♀ imago, paralectotype ♂

and ♀ imagos from type-colony, CONGO: Brazzaville (*J. Weiss*), in Silvestri Coll., Istituto di Entomologia Agraria, Portici, Naples.

Other material. GUINEA: Mount Nimba (*M. Lamotte*) in AMNH and BMNH. DEMOCRATIC REPUBLIC OF CONGO: Yangambi, 29.v.1948, Camp Putnam, Epulu R., v.1948 (*A. E. Emerson*) in AMNH.

There is no biological information relating to the five known nest-series.

Astratotermes prosenus sp. n.

(Text-figs 278, 279, 284, 285 & 298-303; Pl. 2, fig. 5)

Imago. Head capsule brown to sepia-brown, darker above ocelli, dark areas often extending as tapering streaks converging to fontanelle; fontanelle fairly large, a little smaller than ocelli, circular or slightly broader than long, sometimes irregular outline, flat or slightly depressed, yellow-white to pale yellow-brown; medial spot circular, flat, smaller than fontanelle, brown; postclypeus yellow-brown, labrum yellow; frontal marks weakly developed, flat crescent, pale yellow-brown to brown; antennae yellow to pale yellow-brown. Pronotum, meso- and metanota brown, transverse sutures distinct; femora yellow-brown, tibiae paler, tarsi yellow, Abdominal tergites brown, dorsal stigmata and sternites, pale brown, sternites paler in middle, ventral stigmata pale; cerci yellow.

Posterior margin of head capsule usually evenly though somewhat broadly rounded; ocelli medium-sized, separated from compound eyes by approximately own least diameter; postclypeus weakly to moderately inflated, Pcl/W, 0.23-0.27, posterior margin arched, median suture distinct. Apical teeth of mandibles fairly long, L_A/L_1 , 0.68-0.78, R_A/R_1 , 0.92-1.06; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio $L_A/L_1.L_m$, 6.34-8.90; points of apical and marginal teeth of right mandible in line, anterior edge of first marginal slightly longer than that of second. Meso- and metanota moderately wide at constriction, M/W, 0.32-0.35. Pilosity of head capsule yellow-brown, rather sparse slightly uneven pelt with emergent setae.

Measurements (six specimens from three localities) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	1.25-1.61	1.394 \pm 0.135
Ocellus ($O_w \times O_1$)	0.09-0.13 \times 0.11-0.19	0.106 \pm 0.014 \times 0.145 \pm 0.028
Ocellus to eye (O-E)	0.09-0.13	0.104 \pm 0.014
Postclypeus length (Pcl)	0.33-0.38	0.352 \pm 0.023
Antennal article III	0.04-0.08	0.057 \pm 0.011
Antennal article IV	0.06-0.09	0.074 \pm 0.008
Antennal article V	0.07-0.09	0.075 \pm 0.008
Left mandible, apical to first marginal (L_A)	0.14-0.18	0.153 \pm 0.016
Left mandible, first to third marginal (L_1)	0.19-0.25	0.215 \pm 0.026
Left mandible, third marginal to molar (L_m)	0.09-0.11	0.094 \pm 0.007
Right mandible, apical to first marginal (R_A)	0.13-0.18	0.159 \pm 0.019
Right mandible, apical to first marginal (R_A)	0.15-0.18	0.159 \pm 0.016



FIGS 286-303. *Astratotermes*, worker mandibles, mesenteric-proctodeal junctions showing attachments of malpighian tubules and positions of malpighian knot, and views of enteric valve seatings. 286-291, *A. mansuetus*; 292-297, *A. pacatus*; 298-303, *A. prosenus*.

Right mandible, second marginal to molar (R_m)	0.08-0.11	0.094 ± 0.015
Mesonotum width (M)	0.43-0.53	0.464 ± 0.034
Metanotum width (N)	0.39-0.56	0.441 ± 0.059

Worker. Head capsule pale yellow, pilosity sparse and long, yellow. Postclypeus moderately inflated, Pcl/W , 0.29-0.31, Pcl/R_1 , 2.38-2.60. Apical teeth of mandibles fairly long, L_A/L_1 , 0.71-0.79, R_A/R_1 , 1.00-1.02; subsidiary marginal teeth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio, $L_A/L_1.L_m$, 11.40-12.55; apical and marginal teeth approximately in line, anterior edge of first marginal distinctly longer than that of second, $R_A/R_1.R_m$, 14.49-14.80. Fore tibia scarcely inflated, Tl/Tw , 5.33-5.42, third apical spur distinct, about half length of other two. Mesenteric overlap at junction with proctodeum diagonal, to right of malpighian knot; enteric valve seating lateral in unopened abdomen, very weakly three-lobed, connected to second pouch of proctodeum by short neck; membranous wall of valve beyond cushions with sparse minute spicules.

Measurements (three specimens from three localities) in millimetres.

	Range
Head width (W)	1.04-1.09
Fore tibia width (T_w)	0.15
Fore tibia length (T_1)	0.80-0.81
Postclypeus length (Pcl)	0.31-0.33
Left mandible, apical to first marginal (L_A)	0.13-0.14
Left mandible, first to third marginal (L_1)	0.18
Left mandible, third marginal to molar (L_m)	0.06
Right mandible, apical to first marginal (R_A)	0.13
Right mandible, first to second marginal (R_1)	0.13
Right mandible, second marginal to molar (R_m)	0.07

All the necessary comparisons between *A. prosenus* and other members of the genus have already been made in their individual descriptions. *Astratotermes prosenus* has been made the type-species of the genus because it is the species most distinct from related genera, and so least likely to sink in synonymy should adjustments be needed in their membership in future. The abdomen of the worker caste appears at least potentially dehiscent in *A. prosenus*.

Holotype ♀ imago, paratype ♂ and ♀ imagos, and workers from type-colony. NIGERIA: Northern Region, 30 miles from Lokoja on Okene Road, 8.iii.1958 (*W. A. Sands* Coll. No. S.2081) in British Museum (Natural History).

Other paratype material. NIGERIA: Northern Region, 6 m. from Gombe on Dadin Kowa Road, 9.v.1957 and Samaru Regional Research Station near Zaria, 18.v.1959 (*W. A. Sands*). Imagos and workers in BMNH.

This species has only been found in the surface layers of low, wide mounds at the base of trees in Guinean savanna, probably built by *Odontotermes* species. Alates were collected at light in May between 6.45 and 7.15 p.m. after an early shower at the start of the rainy season.

ALYSCOTERMES gen. n.

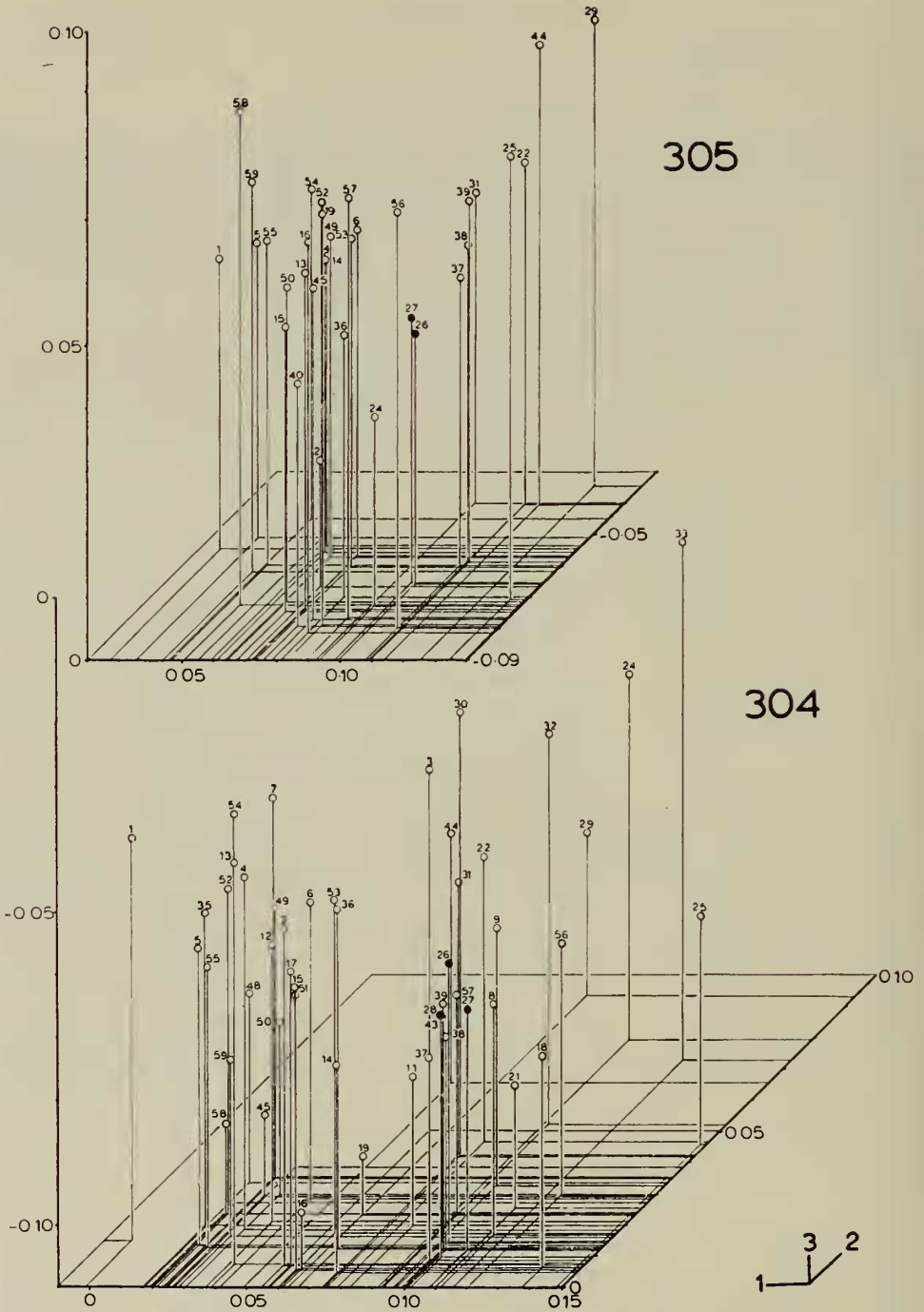
(Alysko, Gr., 'flee from, shun, wander')

Type-species: *Alyscotermes kilimandjaricus* (Sjöstedt)

Imago. Medium sized to large, W, 0.90–1.35. Fore tibia with three apical spurs, third only slightly smaller than other two. Apical teeth of mandibles fairly short, L_A/L_1 , 0.49–0.66, R_A/R_1 , 0.67–0.99; subsidiary marginal tooth of left mandible distinctly separated from molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 4.87–10.50. Right mandible with points of apical and marginal teeth more or less in line, anterior edge of first marginal distinctly longer than that of second. Meso- and metanota vary from moderately to distinctly wide at constriction, M/W, 0.28–0.37, transverse dark sutures present, usually distinct; complex ratio of mandible and notal measurements $L_1/M.N.$, 0.84–1.85.

Worker. Medium sized to very large, W, 0.81–1.11. Fore tibia slender, T_1/T_w , 5.28–7.36, with three apical spurs, third usually well developed, sometimes reduced, never vestigial. Apical teeth of mandibles short, L_A/L_1 , 0.50–0.67, R_A/R_1 , 0.66–0.87; subsidiary marginal tooth of left mandible separated from molar prominence by deep notch in surface view, complex ratio, $L_A/L_1.L_m$, 6.42–12.75. Right mandible with apical and marginal teeth in line, anterior edges of marginal teeth subequal or first slightly longer, complex ratio, $R_A/R_1.R_m$, 10.13–15.40. Mesenteric junction with proctodeum diagonal, to right of malpighian knot. Enteric valve seating distinctly two-lobed, sometimes with very weakly developed third, connected to second pouch of proctodeum by definite neck, dorsolateral in unopened abdomen. Internal cushions of enteric valve unequally developed, positions 1 and 2 retracted, 3 and 4 slightly longer, produced through valve opening; all cushions armed with spines, minute in mesal third, small to pronounced in distal third, protruding through valve opening, particularly in positions 3 and 4.

The characteristic enteric valve armature of the worker caste makes this genus an easy one to recognize. A very few specimens of *A. kilimandjaricus* have been found in which it was less well developed and could only be seen after mounting and clearing, but in general the character can be seen at magnifications of around 100 × unmounted, in alcohol. Only in *Amalotermes* is the enteric valve somewhat similarly armed, but in this the small, brown-headed workers are distinctive, and the armature of the valve is approximately radially symmetrical. All the other genera with armed valves have their distinctive patterns which are illustrated. In the imago identification is more difficult. Of the genera with overlapping size-range and three apical spurs on the fore tibia, *Adynatotermes* has differently proportioned mandibles, as also do *Acholotermes*, *Aganotermes*, *Asagarotermes* and *Amicotermes*. The confusion arises with some members of *Astratotermes* and *Astalotermes* of Groups II and III. No satisfactory key character has been found to separate these from *Alyscotermes*. However, the individual species can be separately distinguished. In *Astratotermes*, *A. aneristus*, *A. apocnetus*, *A. hilarus* and *A. mansuetus* have the anterior edge of the right second marginal at least as long as the first. *A. pacatus* has large eyes and ocelli and *A. prosenus* longer apical teeth and conspicuous fontanelle. In *Astalotermes*, the most difficult species is *A. hapalus*, which very closely resembles *Alyscotermes* in the imago. The only differences are small ones in the proportions of the mandibles when compared with specimens from nearby localities, and the slightly more narrowly rounded head capsule and postclypeus. *A. aganus* and *A. mitis* both have a distinctly depressed pale fontanelle, and again, slightly different mandibles. *A. ignavus* and *A. murcus* both have very long head



FIGS 304 & 305. Three-dimensional graphs of canonical variates 1, 2 & 3, showing species of *Alyscotermes* as solid spots. 304, imago; 305, worker caste.

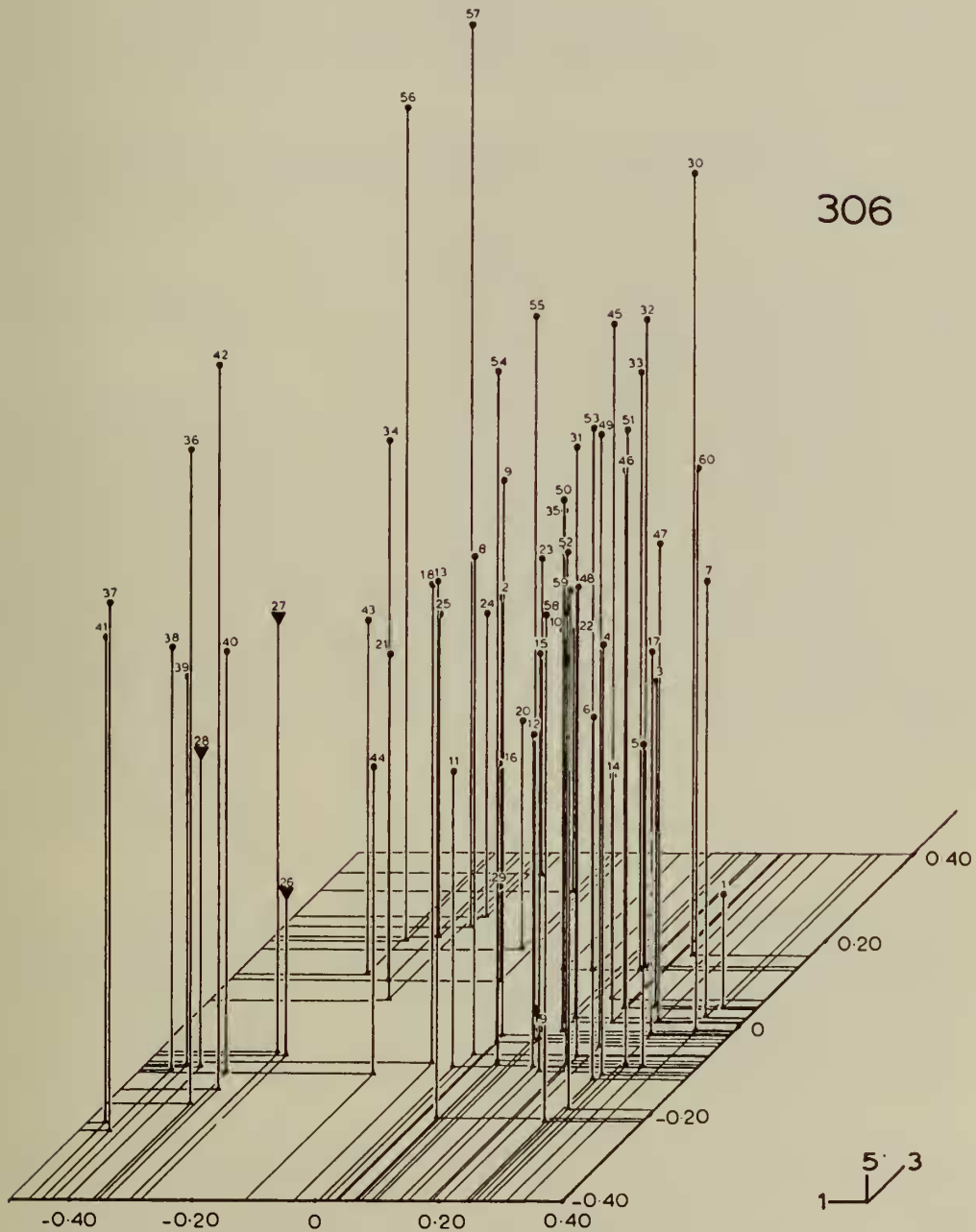


FIG. 306. Three-dimensional graph of principal co-ordinates analysis-plots of eigenvectors 1, 3 & 5 showing species of *Alyscotermes* marked by large triangles. *A. kilimandjaricus* is represented by two points as in cluster analysis.

setae. In *A. brevior* and *A. quietus*, the right first marginal is reduced, and shorter than the second. In *A. empodius* it is the subsidiary marginal tooth of the left mandible which is scarcely clear of the molar prominence; the fontanelle is pale and depressed. *A. irrixosus* is again very similar to *Alyscotermes* and was at first placed in that genus. The absence of enteric valve armature is in this case the only distinguishing feature.

Clearly *Astalotermes* and *Alyscotermes* are closely related, and, as indicated in the discussion on *Astalotermes*, other ways of delimiting genera to take account of this have been considered. The results of the principal co-ordinate analysis separate them, as do the cluster analyses. In order to be consistent with the results for some better defined genera, they are named as separate taxa. In the numerical analyses, *Alyscotermes* is placed nearest to *Ateuchotermes*. (Text-figs 304, 305 & 306 to be compared with Text-figs 400, 401 & 402.) The latter genus has a distinctive enteric valve and no confusion can arise between them.

The name of this genus refers to the frequency with which it has displayed the behaviour described by Grassé & Noirot (1951) as 'La sociotomie'. Entire colonies have been found migrating complete with physogastric queen over the soil-surface. This usually results from an attack by burrowing Doryline ants. The termites flee from their beleaguered nest tunnels and wander about looking for a new home.

No key is provided since the genus contains only two species, and presents no problem of identification once the generic identity of a specimen is recognized. *A. kilimandjaricus* (Sjöstedt) is widespread and common, *A. trestus* sp. n. is only known from one nest-series. It is distinguished from its commoner congener by the much more spiny enteric valve armature and slightly differently proportioned mandibles of the worker caste. The only difference in the imago of *A. trestus* is the more evenly rounded postclypeus.

Alyscotermes kilimandjaricus (Sjöstedt) **comb. n.**

(Text-figs 307-310 & 315-320; Pl. 2, figs 8-11)

Eutermes kilimandjaricus Sjöstedt, 1907: 9. LECTOTYPE ♀, TANZANIA: Kilimandjaro, Kibonoto (Naturhistoriska Riksmuseum, Stockholm), here designated [examined].

Mivotermes (*Cubitermes*) *natalensis* Holmgren, 1913: 355. Type-series, REPUBLIC OF SOUTH AFRICA: Natal, Amanzimtoti (1 ♀ syntype [examined] in American Museum of Natural History; rest of type-series in Mus. Göttenborg). **Syn. n.**

Mivotermes (? *Procubitermes*) *mfolozii* Fuller, 1925: 190. LECTOTYPE ♂, REPUBLIC OF SOUTH AFRICA: Zululand, White Mfolosi River, Conjeni (National Collection of Isoptera, Pretoria), here designated [examined]. **Syn. n.**

Imago. Head capsule sepia to very dark sepia or chestnut-brown; sometimes darker above ocelli; fontanelle broad to somewhat elongate oval, flat, ridged in middle or slightly raised smaller to distinctly larger than ocellus, orange-yellow to dark sepia-brown; medial spot flat or slightly raised, oval, smaller than fontanelle, coloured as head or a little paler; postclypeus yellow-brown to sepia-brown, labrum yellow to brown; frontal marks flat or slightly depressed crescents, distinctly paler than head; antennae yellow-brown to sepia-brown. Pronotum brown to dark sepia, meso- and metanota brown, transverse dark sutures variable, weak to distinct; femora pale yellow-brown to brown, tibiae paler, tarsi yellow. Abdominal tergites

brown to dark sepia-brown, dorsal stigmata paler or as tergites, sternites and ventral stigmata brown, sternites paler in middle, cerci yellow to pale brown.

Posterior margin of head capsule evenly rounded, or not quite so, slightly undulating; ocelli medium-sized, separated from compound eyes by from less than half to slightly more than own least diameter; postclypeus weakly to strongly inflated, Pcl/W, 0.20-0.34, posterior margin rarely evenly rounded, usually bowed in middle, median suture distinct. Pilosity of head capsule yellow-brown to brown, variable from fine, sparse, short slightly uneven pelt with emergent setae, to uneven, no pelt. Other characters as in generic diagnosis.

Measurements. ('*A. kilimandjaricus*' represented by 24 specimens from 16 localities, '*A. natalensis*' by 25 specimens from 12 localities—see discussion following descriptions) in millimetres.

'A. kilimandjaricus'

	Range	Mean \pm S.D.
Head width across eyes (W)	0.90-1.35	1.146 \pm 0.117
Ocellus ($O_w \times O_1$)	0.07-0.13 \times 0.10-0.17	0.094 \pm 0.014 \times 0.125 \pm 0.018
Ocellus to eye (O-E)	0.04-0.10	0.063 \pm 0.015
Postclypeus length (Pcl)	0.22-0.34	0.289 \pm 0.029
Antennal article III	0.02-0.08	0.045 \pm 0.013
Antennal article IV	0.04-0.09	0.064 \pm 0.016
Antennal article V	0.04-0.09	0.064 \pm 0.015
Left mandible, apical to first marginal (L_A)	0.08-0.11	0.097 \pm 0.007
Left mandible, first to third marginal (L_1)	0.14-0.20	0.172 \pm 0.016
Left mandible, third marginal to molar (L_m)	0.06-0.10	0.085 \pm 0.013
Right mandible, apical to first marginal (R_A)	0.09-0.11	0.100 \pm 0.006
Right mandible, first to second marginal (R_1)	0.10-0.15	0.128 \pm 0.014
Right mandible, second marginal to molar (R_m)	0.06-0.11	0.083 \pm 0.013
Mesonotum width (M)	0.28-0.49	0.370 \pm 0.056
Metanotum width (N)	0.29-0.50	0.374 \pm 0.056

'A. natalensis'

	Range	Mean \pm S.D.
Head width across eyes (W)	1.06-1.30	1.177 \pm 0.064
Ocellus ($O_w \times O_1$)	0.07-0.10 \times 0.09-0.13	0.084 \pm 0.009 \times 0.109 \pm 0.013
Ocellus to eye (O-E)	0.05-0.10	0.068 \pm 0.013
Postclypeus length (Pcl)	0.25-0.44	0.295 \pm 0.039
Antennal article III	0.03-0.06	0.044 \pm 0.008
Antennal article IV	0.05-0.08	0.062 \pm 0.009
Antennal article V	0.05-0.08	0.061 \pm 0.007
Left mandible, apical to first marginal (L_A)	0.09-0.12	0.101 \pm 0.006
Left mandible, first to third marginal (L_1)	0.16-0.20	0.176 \pm 0.010
Left mandible, third marginal to molar (L_m)	0.07-0.10	0.083 \pm 0.007
Right mandible, apical to first marginal (R_A)	0.09-0.11	0.100 \pm 0.006

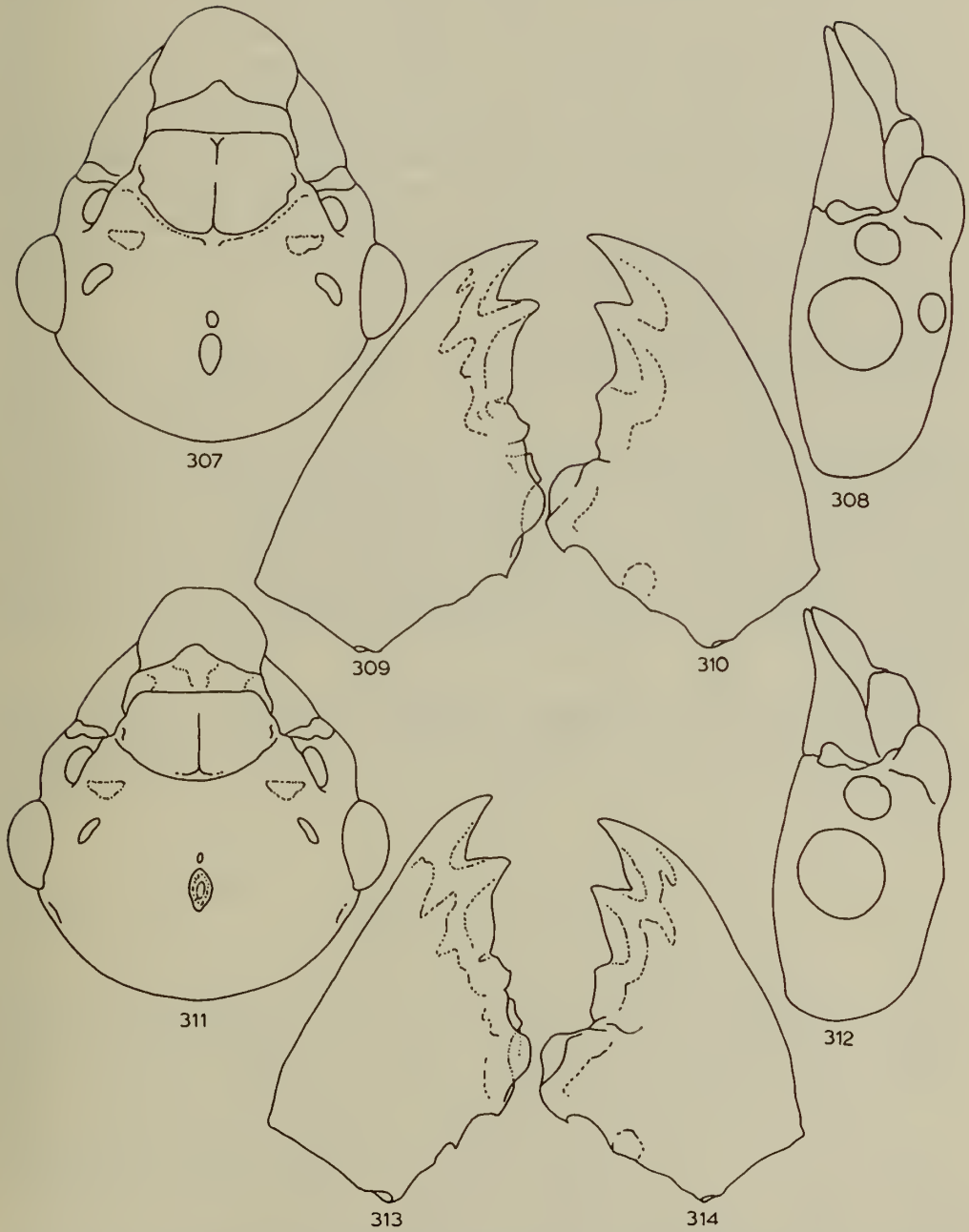
Right mandible, first to second marginal (R_1)	0·11–0·15	0·129 ± 0·009
Right mandible, second marginal to molar (R_m)	0·08–0·10	0·082 ± 0·006
Mesonotum width (M)	0·30–0·44	0·365 ± 0·036
Metanotum width (N)	0·30–0·43	0·369 ± 0·037

Worker. Head capsule yellow-white to yellow, pilosity yellow, sparse. Postclypeus weakly to moderately inflated, Pcl/W, 0·21–0·29, Pcl/ R_1 , 1·89–2·71. Left mandible with subsidiary marginal tooth about same size as third marginal, separated from molar prominence by wide deep notch in surface view, complex ratio, $L_A/L_1.L_m$, 7·90–12·75, anterior edges of first and second marginal teeth of right mandible equal, $R_A/R_1.R_m$, 10·49–15·40. Enteric valve armature in cushion position 3 with 1–9 (only two recorded with more than five) pronounced spines, position 4 sometimes not produced through valve opening, rarely with more than one pronounced spine of ten only small spines, both positions with further small or minute spines; positions 1 and 2 with a few small spines, or all spines minute. Membranous wall of valve beyond cushions with minute spicules. Other characters as in generic diagnosis.

Measurements (in millimetres).

	' <i>A. kilimandjaricus</i> '		' <i>A. natalensis</i> '	
	Range	Mean ± S.D.	Range	Mean ± S.D.
Head width (W)	0·81–1·05	0·934 ± 0·069	0·84–1·00	0·925 ± 0·051
Fore tibia width (T_w)	0·09–0·14	0·114 ± 0·010	0·11–0·13	0·115 ± 0·007
Fore tibia length (T_1)	0·56–0·84	0·689 ± 0·090	0·63–0·71	0·678 ± 0·030
Postclypeus length (Pcl)	0·19–0·33	0·268 ± 0·032	0·21–0·26	0·235 ± 0·017
Left mandible, apical to first marginal (L_A)	0·08–0·10	0·088 ± 0·005	0·08–0·09	0·087 ± 0·006
Left mandible, first to third marginal (L_1)	0·13–0·16	0·148 ± 0·010	0·13–0·15	0·143 ± 0·007
Left mandible, third marginal to molar (L_m)	0·05–0·07	0·060 ± 0·007	0·05–0·06	0·058 ± 0·005
Right mandible, apical to first marginal (R_A)	0·08–0·09	0·087 ± 0·005	0·07–0·09	0·083 ± 0·006
Right mandible, first to second marginal (R_1)	0·09–0·12	0·109 ± 0·008	0·09–0·11	0·103 ± 0·006
Right mandible, second marginal to molar (R_m)	0·05–0·07	0·060 ± 0·005	0·05–0·06	0·060 × 0·004

The essential differences between *A. kilimandjaricus* and *A. trestus* have been mentioned under the generic heading in lieu of a key. The two are clearly very closely related, and *A. trestus* appears to be a local species that has arisen in the anomalous and ecologically isolated area of the Mara forest. *A. kilimandjaricus* has the widest distribution of any of the species in this monograph. It is found from the Gambia in West Africa to Cape Province in South Africa, and in consequence has one of the longest ranges of any African termite. Until a late stage in the present work it was regarded as two species, *A. kilimandjaricus* for the northern specimens and *A. natalensis* for the southern. Slight differences in shape, pilosity and in the gut-characters were thought to occur between them, and were coded accordingly for their separate inclusion in the similarity analysis. However, re-assessment of these features took place when it became necessary to key out the two species. No clear distinction could be made between them on any character or combination of characters and there are not sufficient differences even to warrant



FIGS 307-314. *Alyscotermes*, imago head capsules, front and side views, and imago mandibles. 307-310, *A. kilimandjaricus*; 311-314, *A. trestus*.

the retention of subspecific divisions. The specimens from West Africa and Uganda have a tendency to slightly more even pilosity, forming a pelt on the imaginal head-capsule, which is also slightly less evenly rounded. In the worker, the northern forms sometimes have traces of a third lobe to the enteric valve seating, a marginally longer mesenteric overlap with the proctodeum, and somewhat weaker enteric valve-armature. There are some indications that these character differences may form a cline. In order to show the close similarity of size and proportions throughout the range, the two groups of measurements are given separately rather than amalgamated. The abdomen of the worker caste is dehiscent in *A. kilimandjaricus*.

A lectotype has been designated below from the existing syntype material of *A. kilimandjaricus* (Sjöstedt), and from the syntypes of its junior synonym *Mirotermes* (*Procubitermes*) *mfolozii* Fuller.

Type-material. *Eutermes kilimandjaricus* Sjöstedt, LECTOTYPE ♀ imago, paralectotype ♂ and ♀ imagos from type-series, TANZANIA: Kilimanjaro, Kibonoto, 17.viii.1905 (*Y. Sjöstedt*), in Naturhistoriska Riksmuseum, Stockholm; paralectotype ♀ in American Museum of Natural History. *Mirotermes* (*Cubitermes*) *natalensis* Holmgren, type-series, REPUBLIC OF SOUTH AFRICA: Natal, Amanzimtoti (*I. Trägårdh*), one ♀ in American Museum of Natural History, rest of type-series in Mus. Göteborg. *Mirotermes* (? *Procubitermes*) *mfolozii* Fuller, LECTOTYPE ♂ imago and paralectotype ♂ imagos from type-colony, REPUBLIC OF SOUTH AFRICA: Zululand, White Mfolozi River, Conjeni, S. bank, 27.iii.1922 (*R. H. Harris*) (Fuller Coll. No. F1288), in N.C.I., Pretoria; other paralectotypes (Fuller Coll. No. F1530), in National Collection of Isoptera, Pretoria and American Museum of Natural History.

Other material. GAMBIA: 35 m. from Bathurst on Brikama Road, 18.ix.1966 (*W. A. Sands*). GUINEA: Mount Nimba, 6.ix.1946 (*M. Lamotte*), AMNH. IVORY COAST: Mount Nimba, Yale, 14.iv.1968 (*G. Josens*). NIGERIA: Northern Region, Adamawa Prov., Tibak Plateau, Donkin (two vials), 24.v.1957 (*W. A. Sands*). DEMOCRATIC REPUBLIC OF CONGO: Albert National Park, Rwindi Camp, 4.v.1948 (*A. E. Emerson*) AMNH; Garamba National Park, 15.iii.1951 (*H. De Saeger*). UGANDA: Kawanda, iv.1949 (*W. V. Harris*); Karamoja District, Moroto, 7.x.1952 (*W. A. Sands*); Kawanda, 17.ii.1968 (*D. J. Greathead*). KENYA: Nairobi, Muthaiga Forest, 21.ix.1950, Muguga, 21.v.1950 (two vials), Meru, Lower Imenti Forest, 15.ii.1952, Muguga, 7.v.1952 (*W. V. Harris*), Muguga, 7.v.1952, Isiolo, 4.i.1953 (*W. A. Sands*); Kwale, Shimba Hills, 15.vi.1952 (*P. B. Kemp*); Kaptagat, 11.v.1954, Muguga, 8.xi.1954 (*R. M. C. Williams*). TANZANIA: Morogoro, 27.iv.1935, 3.iii and 8.v.1927 (*W. V. Harris*); Babati, Bereku Ridge, 20.iii.1951, Shume, W. Usambara, 20.x.1951, Mombo, Soni, 11.x.1951, Mgera, 25.ii.1952. Daluni, near Amani, 1.iv.1952 (*P. B. Kemp*). MALAWI: Chisenga, S. of Fort Hall, 5.viii 8 m. E. of Cholo on Mlanje Road, 18.viii, Vipya Plateau, 20.ix, 27 m. from Nkata Bay on Ekwendeni Road, 2.ix and 1 m. N. of Chisenga, 2.x.1953 (*W. A. Sands & W. Wilkinson*); Mlanje Mountain, vii-ix and Zomba Mountain, ix.1956 (*A. W. R. McCrae*). RHODESIA: Matopos (three vials), 23-24.i and 8.iii.1966 (*M. G. Bingham*); Salisbury, 10.i.1967 (*R. N. H. Smithers*). REPUBLIC OF SOUTH AFRICA: Transvaal, Pretoria,

21.x.1916 and 9.v.1917 (*C. Fuller*); 26 m. S. of Johannesburg, 9.iv.1935 (*H. Kirby*), AMNH; Pretoria, 6.v.1938, Sibasa, 9.vii.1960 (*W. G. H. Coaton*); Belfast, 27.iv, Ermelo (three vials), 3-6.vi.1956 (*J. H. Grobler*); Rustenburg (two vials), 26.i and Middelburg, 22.iv.1960 (*P. C. Joubert*); Bronkhorstspuit, 11.iii.1962 (*J. L. Sheasby*), N.C.I., Pretoria. Natal, Haviland Rail (two vials), Estcourt, 1894 (*G. D. Haviland*); Charlestown (*I. Trägårdh*); Hilton Road, 1913 (*E. Warren*); Tongaat, 19.iv.1914 (*C. Fuller*), all AMNH; Nkandhla (three vials), 27-28.i.1957, Mahlabatini, 6.xii, Umzimkulu, 17.xii, Lions River, 19.xii and Bergville, 21.xii.1959 (*P. C. Joubert*); Impendhle, 21.i.1962 (*J. L. Sheasby*); Orange Free State, Heilbron, 22.v.1938 (*W. G. H. Coaton*) all N.C.I., Pretoria; Cape Province, Kentani, iv.1918 (*A. Pegler*); Zwartkop, 7 m. from Port Elizabeth, 20.iii.1914 (*Anon.*), N.C.I. and AMNH; Port St. Johns, 14.iii.1938, Albany, 26.i.1958, Somerset East, 7.ii.1961 (*W. G. H. Coaton*), Albany (five vials), 12.viii.1951, 20.vi and 1.xi.1955, 9.vi.1957 and 29.vii.1961 (*E. McCallan, J. Myers, F. W. Gess*); Umzimkulu, 20.i, Qumbu, 10.x and Flagstaff, 12.x.1962 (*J. L. Sheasby*); Tsolo, 15.x and Komgha, 22.x.1962 (*G. F. Pretorius*), all in N.C.I., Pretoria.

Specimens listed above are in the BMNH unless otherwise stated. Eighty-four nest-series have been examined and something is known of the biology. The species does not construct a mound, but has been found in the mounds of *Cubitermes*, under rocks, and swarming from subterranean tunnels. Many of the records are from high altitudes, up to 8000 feet above sea level. In general it appears commonest in fairly moist savanna, often adjacent to rain forest, though a few records are from drier areas. This species appears to be more ready than most termites to leave its underground nest system to wander on the surface. On a number of occasions (at least five) it has been recorded on the march complete with reproductive castes; this behaviour usually results from attacks by burrowing Doryline ants, and in one instance the species of ant has been identified as *Rhognus fimbriatus* (Shuckard).

Alyscotermes trestus sp. n.

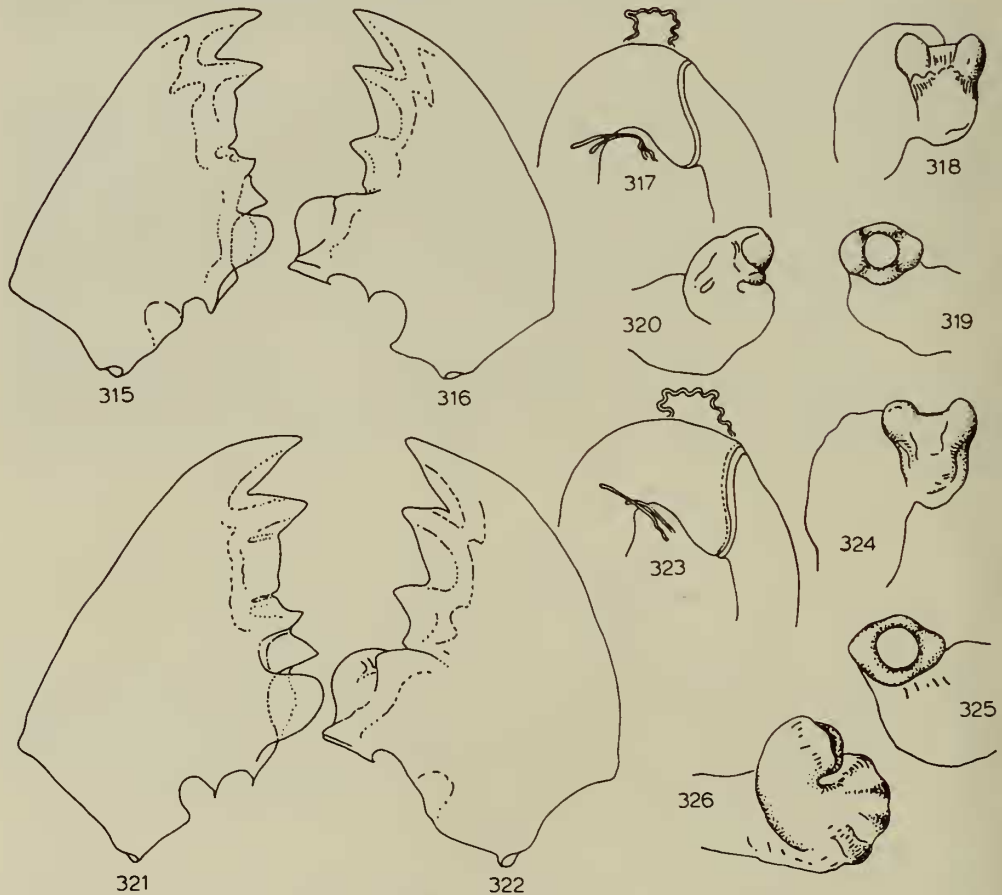
(Text-figs 311-314 & 321-326; Pl. 2, figs 6 & 7)

Imago. Head capsule dark chestnut-brown, very dark above ocelli; fontanelle oval, flat, slightly raised, or depressed in middle, somewhat roughened, a little smaller than ocellus-chestnut-brown; medial spot circular or short oval, slightly distinct, slightly depressed chestnut, brown, semicircular; antennae sepia-brown. Pronotum, meso- and metanota chestnut-brown. Transverse dark sutures distinct; femora sepia-brown, tibiae paler, tarsi yellow-brown. Abdominal tergites and dorsal stigmata, chestnut-brown, sternites and ventral stigmata brown, sternites yellow-brown in middle; cerci pale yellow-brown.

Posterior margin of head capsule not quite evenly rounded, slightly undulating; ocelli small, separated from compound eyes by own least diameter or slightly more; postclypeus weakly inflated, Pcl/W, 0.22-0.25, posterior margin broadly and evenly rounded, median suture distinct. Pilosity of head capsule brown, coarse pelt obscured by numerous uneven emergent setae. Other characters as in generic diagnosis.

Measurements (two specimens from one colony) in millimetres.

Head width across eyes (W)	1.22-1.29
Ocellus ($O_w \times O_l$)	0.09-0.10 \times 0.11
Ocellus to eye (O-E)	0.09-0.12
Postclypeus length (Pcl)	0.29-0.30
Antennal article III	0.04-0.05
Antennal article IV	0.05-0.06
Antennal article V	0.06
Left mandible, apical to first marginal (L_A)	0.10-0.11
Left mandible, first to third marginal (L_l)	0.18
Left mandible, third marginal to molar (L_m)	0.09
Right mandible, apical to first marginal (R_A)	0.10-0.11



FIGS 315-326. *Alyscotermes*, worker mandibles, mesenteric-proctodeal junctions showing attachments of malpighian tubules and positions of malpighian knot, and views of enteric valve seatings. 315-320, *A. kilimandjaricus*; 321-326, *A. trestus*.

Right mandible, apical to second marginal (R ₁)	0.13
Right mandible, second marginal to molar (R _m)	0.09-0.10
Mesonotum width (M)	0.40-0.46
Metanotum width (N)	0.39-0.46

Worker. Head capsule yellow, pilosity sparse and scattered, orange. Postclypeus moderately inflated, Pcl/W, 0.27, Pcl/R₁, 2.37. Left mandible with subsidiary marginal tooth larger and more prominent than third marginal, separated from molar prominence by wide deep notch in surface view, complex ratio, L_A/L₁.L_m, 6.42; first marginal tooth of right mandible with anterior edge slightly longer than that of second, R_A/R₁.R_m, 10.13. Enteric valve armature of positions 3 and 4 with 7-12 pronounced spines, carried on slightly sclerotized cushions, and many small and minute spines; positions 1 and 2 with 1-3 pronounced spines, cushions unsclerotized, many small and minute spines. Membranous wall of valve beyond cushions with minute spicules. Other characters as in generic diagnosis.

Measurements (one specimen) in millimetres.

Head width (W)	1.11
Fore tibia width (T _w)	0.13
Fore tibia length (T _l)	0.78
Postclypeus length (Pcl)	0.30
Left mandible, apical to first marginal (L _A)	0.10
Left mandible, first to third marginal (L ₁)	0.17
Left mandible, third marginal to molar (L _m)	0.09
Right mandible, apical to first marginal (R _A)	0.11
Right mandible, first to second marginal (R ₁)	0.13
Right mandible, second marginal to molar (R _m)	0.08

The distinguishing features of *A. trestus* have already been discussed in comparison with *A. kilimandjaricus*. The asymmetrical development of the enteric valve armature in the worker may represent an early stage in the development of a valve like that of *Anaoterмес*. The abdomen of the worker caste shows signs of being dehiscent in some specimens.

Holotype ♀ imago, paratype ♂ and ♀ imagos, and workers from type-colony, KENYA: Narok District, Mara, 9 miles from Olokurto, 16.v.1961 (*P. E. Glover*) coll. No. G7553) in British Museum (Natural History).

There is no biological information on the single known nest-series.

AGANOTERMES gen. n.

(Aganos, Gr., 'mild, gentle')

Type-species: *Aganotermes oryctes* sp. n.

Imago. Large-sized, W, 1.11-1.23. Fore tibia with three apical spurs, third well developed, a little shorter than other two. Apical teeth of mandibles long, L_A/L₁, 0.79-0.83, R_A/R₁, 1.11-1.19; subsidiary marginal tooth of left mandible with proximal end just level with edge

of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 10.41-12.04. Points of apical and marginal teeth of right mandible in line, anterior edge of first marginal longer than that of second. Meso- and metanota narrow at constriction, M/W , 0.21-0.24, transverse dark sutures absent.

Worker. Large, W , 0.86-0.94. Fore tibia scarcely swollen, T_1/T_w , 5.00-5.53, with three apical spurs, third about one-third length of other two. Apical teeth of mandibles very long, L_A/L_1 , 0.97-1.00, R_A/R_1 , 1.25-1.29; subsidiary tooth of left mandible with proximal end level with edge of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 25.81-26.66; points of apical and marginal teeth of right mandible in line, anterior edge of first marginal longer than that of second, complex ratio, $R_A/R_1.R_m$, 25.40-30.25. Mesenteric overlap at junction with proctodeum twice width of mesenteron at insertion of malpighian tubules or a little more, proximal end of proctodeum within malpighian knot, towards left side. Enteric valve seating with two very weak lobes, connected to second pouch of proctodeum by very short neck, ventral in position in unopened abdomen; internal cushions of enteric valve without armature, surface scaly.

This is again a monotypic genus, slightly related to *Adynatotermes*, and perhaps to some species of *Astalotermes*, but readily recognizable by its long mandibular apical teeth. In this respect it resembles the next genus, *Acholotermes*, but the meso- and metanota of the imago are narrower, and the ocelli much more distant from the compound eyes. In the worker, the enteric valve seating has a much shorter neck, and is more ventral in the unopened abdomen. The only other genera with equally long apical teeth are *Asagarotermes* and *Amicotermes*. In the imagos these have the left subsidiary marginal tooth clear of the molar prominence, the ocellus closer to the eye, and a more inflated postclypeus. The workers of these genera each have uniquely characteristic enteric valve armature. In the results of the analysis of the similarity matrix, the principal co-ordinates place *Aganotermes* near the rather large, loose cloud of points that form the genus *Astalotermes*, and fairly close to *Adynatotermes*. The cluster analyses both bring it out very late, remaining independent in the single linkage down to the 78% phenon level, joining after *Astalotermes obstructus* and before another monotypic genus, *Amicotermes*. When clustered by median sorting, it remains unattached until the last five places, four of which form monotypic genera, at the 70% phenon line. In the canonical variates analysis based on measurements alone, *Aganotermes* is one of the most isolated genera.

Aganotermes oryctes sp. n.

(Text-figs 327-336; Pl. 2, fig. 12)

Imago. Head capsule sepia-brown to very dark sepia-brown, definitely darker above ocelli, dark often extending as tapering streaks converging to fontanelle; fontanelle very small, oval, depressed, coloured as head capsule; medial spot as large as or larger than fontanelle, oval, paler than head capsule, raised on distinct bump; postclypeus, slightly paler than head capsule, labrum, yellow-brown to brown, frontal marks semicircular, flat, paler than head; antennae yellow-brown to sepia-brown. Pronotum, brown to dark sepia-brown, meso- and metanota brown; femora pale yellow-brown to brown, tibiae paler, tarsi yellow. Abdominal tergites brown to sepia-brown, dorsal stigmata darker, sternites brown, paler in mid-line, stigmata darker; cerci very pale brown.

Posterior margin of head capsule not quite evenly rounded, slightly undulating; ocelli rather small, separated from compound eyes by much more than own least diameter; postclypeus

moderately inflated, Pcl/W, 0.24-0.28, posterior margin bowed, not evenly rounded, median suture distinct; pilosity of head capsule dense, uneven, rather coarse, not forming a pelt. Other characters given in generic diagnosis.

Measurements (six specimens from three localities) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	1.11-1.23	1.150 \pm 0.031
Ocellus ($O_w \times O_l$)	0.08-0.09 \times 0.09-0.13	0.080 \pm 0.015 \times 0.102 \pm 0.015
Ocellus to eye (O-E)	0.09-0.13	0.112 \pm 0.010
Postclypeus length (Pcl)	0.28-0.31	0.296 \pm 0.013
Antennal article III	0.06-0.08	0.067 \pm 0.005
Antennal article IV	0.07-0.09	0.077 \pm 0.004
Antennal article V	0.07-0.08	0.077 \pm 0.004
Left mandible, apical to first marginal (L_A)	0.14-0.16	0.153 \pm 0.005
Left mandible, first to third marginal (L_1)	0.18-0.20	0.189 \pm 0.007
Left mandible, third marginal to molar (L_m)	0.07-0.08	0.074 \pm 0.004
Right mandible, apical to first marginal (R_A)	0.15-0.17	0.158 \pm 0.007
Right mandible, first to second marginal (R_1)	0.13-0.15	0.138 \pm 0.007
Right mandible, second marginal to molar (R_m)	0.07-0.09	0.077 \pm 0.004
Mesonotum width (M)	0.24-0.28	0.257 \pm 0.014
Metanotum width (N)	0.22-0.27	0.243 \pm 0.018

Worker. Head capsule very pale yellow, pilosity dense, with long conspicuous coarse yellow setae. Postclypeus strongly inflated, Pcl/W, 0.35-0.36; Pcl/ R_1 , 3.25-3.50. Membranous wall of enteric valve beyond cushions apparently without even minute spicules. Other characters in generic diagnosis.

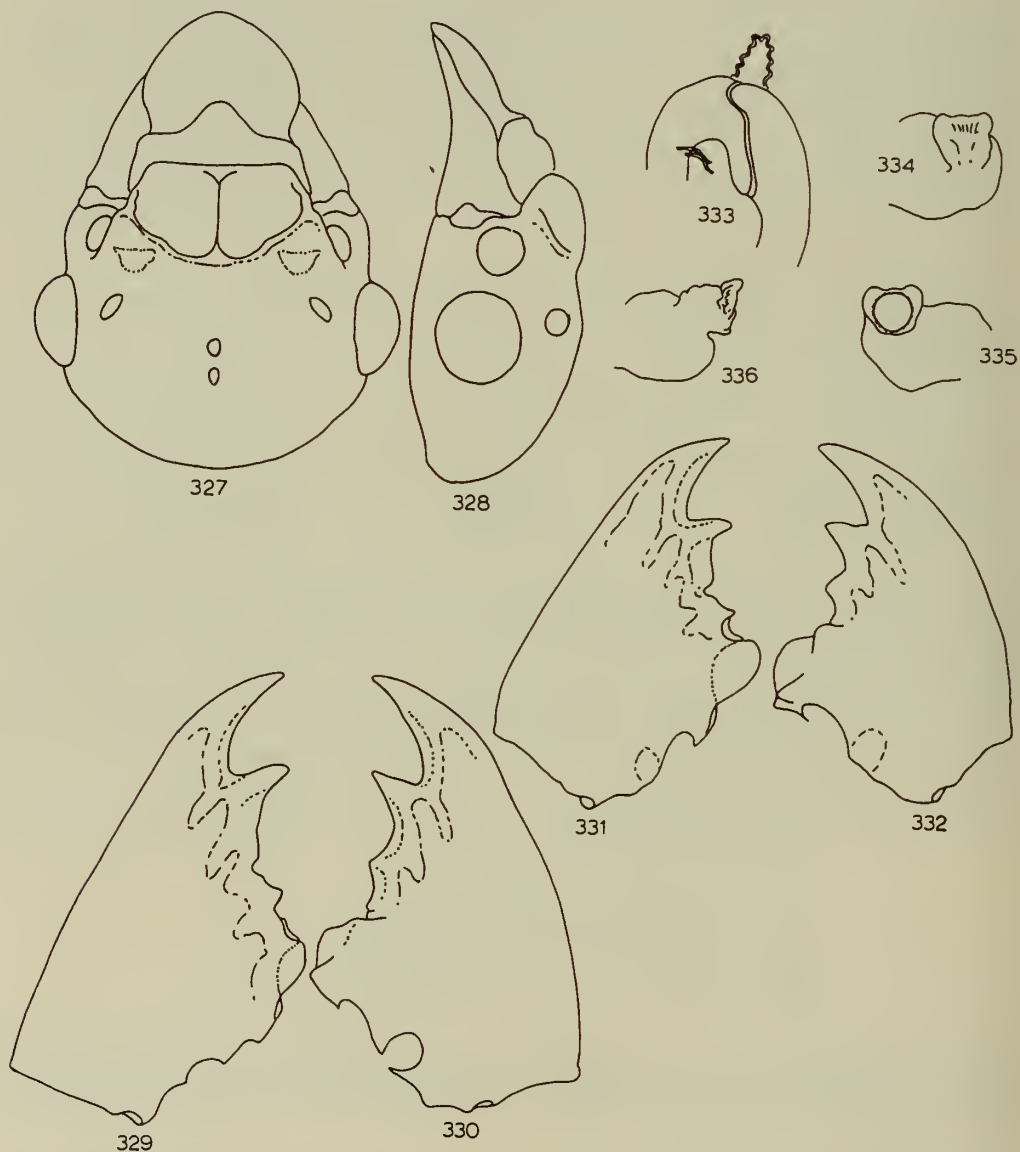
Measurements (two specimens from two localities) in millimetres.

Head width (W)	0.86-0.94
Fore tibia width (T_w)	0.11-0.13
Fore tibia length (T_l)	0.59-0.63
Postclypeus length (Pcl)	0.30-0.33
Left mandible, apical to first marginal (L_A)	0.13
Left mandible, first to third marginal (L_1)	0.13
Left mandible, third marginal to molar (L_m)	0.04
Right mandible, apical to first marginal (R_A)	0.11-0.13
Right mandible, first to second marginal (R_1)	0.09-0.10
Right mandible, second marginal to molar (R_m)	0.04-0.06

The relationships of this species, and its distinguishing features, have already been discussed under the generic heading. The abdomen of the worker caste appears to be dehiscent in *Aganotermes oryctes*.

Holotype ♀ imago, paratype ♂ and ♀ imagos, and workers from type-colony, REPUBLIC OF SOUTH AFRICA: Transvaal, Letaba, 10.ii.1964 (*W. G. H. Coaton*) in National Collection of Isoptera, Coll. No. TM.13,333, Pretoria; paratypes from type-colony also in BMNH.

Other paratype material, REPUBLIC OF SOUTH AFRICA: Transvaal, Warmbaths, 12.ii.1963 (*W. G. H. Coaton*). RHODESIA: Matopos: Research Station, 20°25'S., 28°30'E., alt. 4,000 ft, 16.xi.1965 and 23.i.1966, Atlantica Research Station, Salisbury district, 16°29'S., 30°14'E., alt. 3,700 ft, 7.xi.1965 (*M. G. Bingham*); Ruwa, Melfort,



FIGS 327-336. *Aganotermes oryctes*. 327, 328, front and side views of imago head capsule; 329, 330, imago mandibles; 331, 332, worker ditto; 333, mesenteric-proctodeal junction showing attachment of malpighian tubules and position of malpighian knot; 334-336, views of enteric valve seating.

17°57'S., 31°16'E., 12.xii.1969 (*B. L. Mitchell*). ZAMBIA: Lusaka, 9.xii.1966 and Chipongwe, 16.xi.1969 (*M. G. Bingham*).

Material in BMNH except where stated otherwise.

The only biological information on this species is that it is found as a 'lodger' in mounds of *Odontotermes* and *Macrotermes*.

ACHOLOTERMES gen. n.

(*Acholos*, Gr., 'meek')

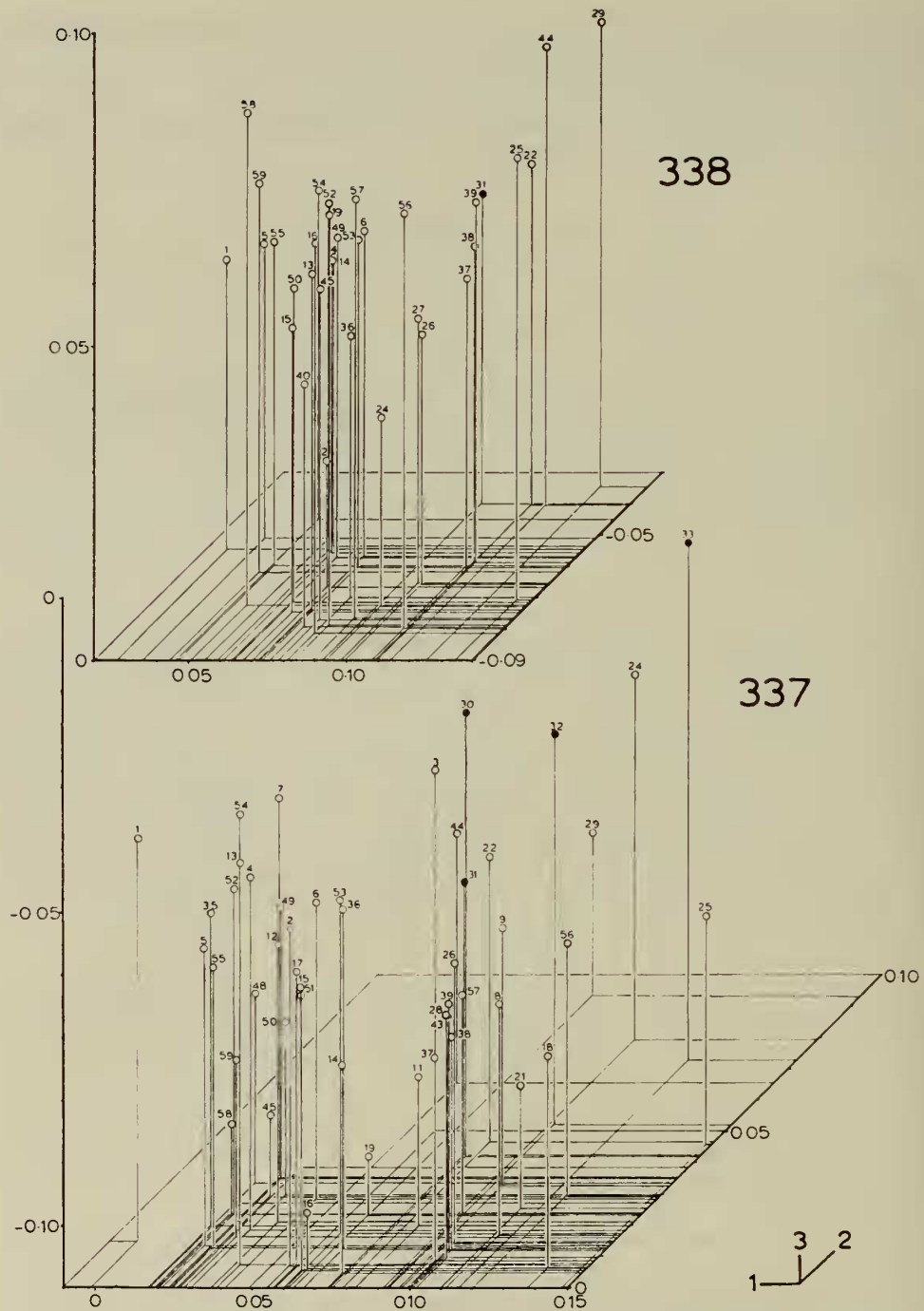
Type-species: *Acholotermes tithasus* sp. n.

Imago. Medium sized, W, 0.84-1.06. Fore tibia with three apical spurs, third small to well developed. Apical teeth of mandibles long, L_A/L_1 , 0.68-1.04, R_A/R_1 , 0.92-1.45; subsidiary marginal tooth of left mandible with proximal end level with edge of molar prominence or just clear of it in surface view, complex ratio, $L_A/L_1.L_m$, 11.59-16.29. Point of first marginal tooth of right mandible slightly to distinctly behind line of apical to second marginal, anterior edge of first marginal equal to or a little longer than that of second. Meso- and metanota rather narrow to somewhat wider at constriction, M/W, 0.25-0.32, transverse dark sutures weak or absent in type-species, present in others; complex ratio of mandible and notal measurements, $L_1/M.N$, 1.26-2.58.

Worker. Medium sized, W, 0.70-0.80. Fore tibia scarcely to moderately swollen, T_1/T_w , 3.91-5.30, with three apical spurs, third usually well developed, small to vestigial in one species. Apical teeth of mandibles long to very long. L_A/L_1 , 0.81-1.07, R_A/R_1 , 0.97-1.29, subsidiary marginal tooth of left mandible just clear of molar prominence in surface view or separated by distinct notch, complex ratio, $L_A/L_1.L_m$, 20.75-22.89; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal shorter than that of second or equal to it, complex ratio, $R_A/R_1.R_m$, 22.80-30.15. Mesenteric junction with proctodeum practically transverse and to right of malpighian knot in three or four species, overlapping by twice width of mesenteron and touching malpighian knot in the fourth. Enteric valve seating distinctly but not prominently three-lobed, connected to second pouch of proctodeum by long neck, lateral to dorso-lateral in position in unopened abdomen; internal cushions of enteric valve with scaly surface, posterior margin of each scale with one or more minute spines or spicules.

Three of the four species of *Acholotermes* form a compact, well defined group with many features in common. The fourth, *A. epius*, with a longer mixed segment and reduced third apical spur of the fore tibia shows resemblances to *Anenteotermes* and *Astalotermes* species. These are reflected in both the single linkage cluster analysis and the principal co-ordinate plots (Text-fig. 339). Median sorting leaves all four species together, with *A. epius* joining the group at a phenon level 10% lower than the linkage between the other species, at the same level of affinity as that of certain members of other genera.

The long apical mandibular teeth of both imago and worker castes serve to distinguish *Acholotermes* from most other genera. Those *Astalotermes* that overlap in this respect are smaller, with narrower meso- and metanota and in the worker have unarmed enteric valves. *Anenteotermes* has one species with similarly long apical teeth, but this too is smaller and has many other differences. Two species of *Astratotermes* that partially overlap in the mandible characters can in fact be



FIGS 337 & 338. Three-dimensional graphs of canonical variates 1, 2 & 3 showing species of *Acholotermes* as solid spots. 337, imago; 338, worker caste.

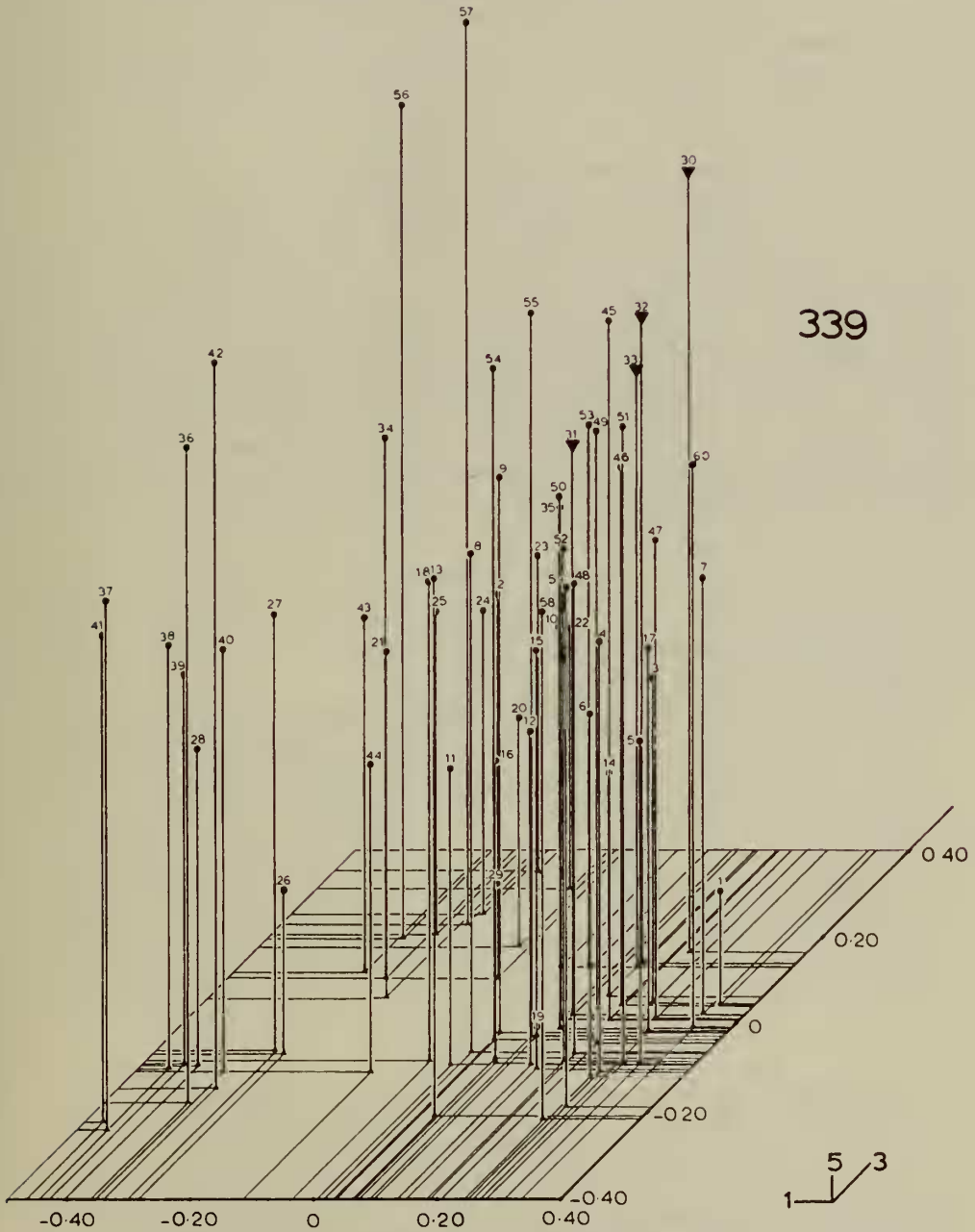


FIG. 339. Three-dimensional graph of principal co-ordinates analysis-plot of eigenvectors 1, 3 & 5 showing species of *Acholotermes* marked by large triangles.

separated in the imago by the complex ratios, or in one of them by the even pilosity and large size; in the worker the complex ratios again serve to separate the genera. The enteric valve cushions of *Astratotermes* have small spines on the posterior parts only, and few spicules or none on the membrane beyond them. In *Acholotermes* the entire enteric valve cushion carries minute spines or multiple spicules fringing the scales, and the membranous wall beyond and between them has a distinct or even thick fringe of spicules. To see those effectively requires phase-contrast illumination and so they are not used in diagnoses or keys. These and the small differences of proportion are enough in the multivariate analysis to separate the *Acholotermes* from the species of *Astratotermes* that resemble it as widely as some very distinctive genera are separated (Text-figs 337, 338 & 339, compare with Text-figs 304-306). In order to achieve consistency of treatment and maintain as far as possible the objectivity imposed by the numerical methods, they are separated with a different generic name. *Aganotermes* has also long apical teeth, but the large size, very narrow meso- and metanota, ocelli distant from the eyes, and the short-necked unarmed enteric valve of the worker all distinguish this genus. There remain only *Amicotermes* and *Asagarotermes* with similar mandibles, both distinguished by the characteristic enteric valve armature of the worker. In the imago the former genus has smaller compound eyes than *Acholotermes*, and *Asagarotermes* has narrower meso- and metanota.

KEYS TO SPECIES

Imagos

- 1 Postclypeus relatively weakly inflated, Pcl/W, 0.23-0.27 2
 - Postclypeus very strongly inflated, Pcl/W, 0.31-0.34 3
 2 Smaller, W, 0.84-0.90. Ocellus separated from compound eye by about half own least diameter, $O_w/O-E$, 1.93-2.04. Apical teeth of mandibles shorter, L_A/L_1 , 0.72-0.82, R_A/R_1 , 1.05 **chiotus** (p. 143)
 - Larger, W, 0.99-1.03. Ocellus separated from compound eyes by almost own least diameter, $O_w/O-E$, 1.04-1.14. Apical teeth of mandibles longer, L_A/L_1 , 0.91-1.04, R_A/R_1 , 1.33-1.45 **tithasus** (p. 149)
 3 Fontanelle short oval, about half diameter of ocellus, paler than head. Apical teeth of mandibles shorter, L_A/L_1 , 0.68-0.76, R_A/R_1 , 0.92-0.99. Mesonotum narrower at constriction, M/W, 0.25-0.28 **epius** (p. 144)
 - Fontanelle vestigial, minute, circular, coloured as head. Apical teeth of mandibles longer, L_A/L_1 , 0.89-0.91. R_A/R_1 , 1.13-1.24. Mesonotum wider at constriction, M/W, 0.30-0.31 **imbellis** (p. 148)

Workers

- 1 Fore tibia slender, T_1/T_w , 5.25-5.30, third apical spur very small, one-quarter or less length of other two. Apical teeth of mandibles shorter, L_A/L_1 , 0.81-0.82. R_A/R_1 , 0.97-1.00. Mesenteric overlap at junction with proctodeum, length twice width of mesenteron at insertion of malpighian tubules **epius** (p. 144)
 - Fore tibia swollen, T_1/T_w , 3.91-4.27, third apical spur one-third or more length of other two. Apical teeth of mandibles longer, L_A/L_1 , 0.89-1.07, R_A/R_1 , 1.11-1.26. Mesenteric junction with proctodeum nearly transverse, slightly angled only, no overlap 2

- 2 Smaller, W, 0.70. Apical teeth of mandibles shorter, L_A/L_1 , 0.89, R_A/R_1 , 1.11. Enteric valve-seating dorso-lateral, near dorsal, in unopened abdomen . . . *chirotus* (p. 143)
- Larger, W, 0.80. Apical teeth of mandibles longer, L_A/L_1 , 1.00–1.07. R_A/R_1 , 1.18–1.29. Enteric valve-seating lateral in unopened abdomen 3
- 3 Postclypeus more strongly inflated, Pcl/W, 0.33. Fore tibia less swollen, T_1/T_w , 4.27 *imbellis* (p. 148)
- Postclypeus less inflated, Pcl/W, 0.28. Fore tibia slightly thicker, T_1/T_w , 3.92 *tithasus* (p. 149)

Acholotermes chirotus sp. n.

(Text-figs 340, 341, 348, 349 & 356–361; Pl. 3, figs 1 & 2)

Imago. Head capsule sepia-brown, darker above ocelli; fontanelle very small, less than one-quarter size of ocellus, nearly flat, circular or short oval, pale brown; medial spot same size and shape as fontanelle, colour as head; postclypeus brown, labrum pale yellow-brown; frontal marks sepia-brown flat crescents; antennae yellow-brown. Pronotum, meso- and metanota, brown, transverse dark sutures present but weak on mesonotum; femora pale yellow brown, tibiae and tarsi yellow. Abdominal tergites brown, dorsal stigmata sepia-brown, sternites yellow-brown, yellow in middle, ventral stigmata brown; cerci yellow.

Posterior margin of head capsule widely and evenly rounded; ocelli fairly large, separated from compound eyes by only about half own least diameter; postclypeus moderately inflated, Pcl/W, 0.25–0.27, posterior margin bowed, not evenly rounded, median suture distinct. Apical teeth of mandibles rather long, L_A/L_1 , 0.72–0.82, R_A/R_1 , 1.05; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 12.88–14.20; point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edge of first marginal approximately equal, to that of second. Pilosity of head capsule sepia-brown, uneven, not forming a pelt. Meso- and metanota fairly wide at constriction, M/W, 0.30. Fore tibia with third apical spur distinct, about one-third length of other two.

Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	0.84–0.90
Ocellus ($O_w \times O_1$)	0.07 × 0.10–0.11
Ocellus to eye (O–E)	0.03
Postclypeus length (Pcl)	0.21–0.24
Antennal article III	0.03
Antennal article IV	0.04
Antennal article V	0.04
Left mandible, apical to first marginal (L_A)	0.09–0.11
Left mandible, first to third marginal (L_1)	0.13
Left mandible, third marginal to molar (L_m)	0.06
Right mandible, apical to first marginal (R_A)	0.10–0.11
Right mandible, first to second marginal (R_1)	0.10
Right mandible, second marginal to molar (R_m)	0.06
Mesonotum width (M)	0.25–0.27
Metanotum width (N)	0.26–0.30

Worker. Head capsule pale yellow, pilosity yellow, fairly numerous setae. Postclypeus moderately inflated, Pcl/W, 0.30. Apical teeth of mandibles long, L_A/L_1 , 0.81, R_A/R_1 , 1.11; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, $L_A/L_1.L_m$, 22.30; anterior edge of first marginal tooth of right mandible shorter than that of second, $R_A/R_1.R_m$, 26.05. Fore tibia moderately swollen, T_1/T_w , 3.91, third apical spur distinct, about one-third length of other two. Mesenteric junction with proctodeum almost transverse, to right of malpighian knot; enteric valve seating dorsolateral in unopened abdomen; internal cushions of enteric valve weakly developed, with scaly surface, posterior margin of each scale fringed with numerous minute spicules. Membranous wall of valve beyond cushions with very numerous rather pronounced spicules arranged in 15-20 rows, broken up into fringed lobes between cushions. Other characters given in generic diagnosis.

Measurements (one specimen) in millimetres.

Head width (W)	0.70
Fore tibia width (T_w)	0.14
Fore tibia length (T_1)	0.54
Postclypeus length (Pcl)	0.21
Left mandible, apical to first marginal (L_A)	0.09
Left mandible, first to third marginal (L_1)	0.10
Left mandible, third marginal to molar (L_m)	0.04
Right mandible, apical to first marginal (R_A)	0.09
Right mandible, first to second marginal (R_1)	0.08
Right mandible, second marginal to molar (R_m)	0.04

A. chirotus is the smallest species in the genus, distinctly smaller than *A. tithasus* with which it is almost certainly sympatric. It also has, in the imago, proportionately larger ocelli closer to the compound eyes, and in both castes, shorter apical mandibular teeth. Both of the savanna species, *A. epius* and *A. imbellis*, have much more inflated postclypeus in the imago. In the worker caste, *A. epius* has a mesenteric overlap with the proctodeum and slender fore tibia; *A. imbellis* has again an inflated postclypeus and longer apical teeth. The worker abdomen of *A. chirotus* appears to be weakly dehiscent.

Holotype ♀ imago, paratype ♂ and ♀ imagos, and workers from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Epulu River, Camp Putnam, 15.v.1948 (*A. E. Emerson*), in American Museum of Natural History. (Paratypes from type-colony, ♂ and ♀ imagos and workers in BMNH.)

The single known nest-series is recorded as having been found in a mound of *Acanthotermes acanthothorax* (Sjöstedt).

Acholotermes epius sp. n.

(Text-figs 342, 343, 350, 351 & 362-367; Pl. 3, fig. 3)

Imago. Head capsule dark sepia-brown, darker above ocelli; fontanelle small, about half size of ocellus, slightly depressed, short-oval, brown, medial spot slightly smaller, flat on slightly raised, short-oval, sepia-brown; postclypeus sepia-brown, labrum yellow-brown; frontal marks sepia-brown, somewhat weakly marked, flat crescents; antennae yellow-brown. Pronotum,

meso- and metanota, sepia-brown, transverse dark sutures distinct; femora yellow-brown, tibiae paler, tarsi yellow. Abdominal tergites sepia-brown with darker dorsal stigmata, sternites brown laterally, pale yellow-brown in middle, ventral stigmata sepia-brown; cerci pale yellow-brown.

Posterior margin of head capsule slightly undulating, not quite evenly rounded; ocelli medium sized, separated from compound eyes by slightly less than half up to two-thirds own least diameter; postclypeus strongly inflated, Pcl/W, 0.31-0.33, posterior margin evenly rounded, median suture strongly developed. Apical teeth of mandibles fairly long, L_A/L_1 , 0.68-0.76, R_A/R_1 , 0.92-0.99; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 11.59-12.18; point of first marginal tooth of right mandible only very slightly behind line of apical to second marginal, anterior edge of first marginal distinctly longer than that of second. Pilosity of head capsule sepia-brown, rough, uneven, not forming a pelt. Meso- and metanota rather narrow at constriction, M/W, 0.25-0.28. Fore tibia with third apical spur vestigial, one-fifth or less length of other two (in type-series, specimens from another colony have them well developed).

Measurements (four specimens from two localities) in millimetres.

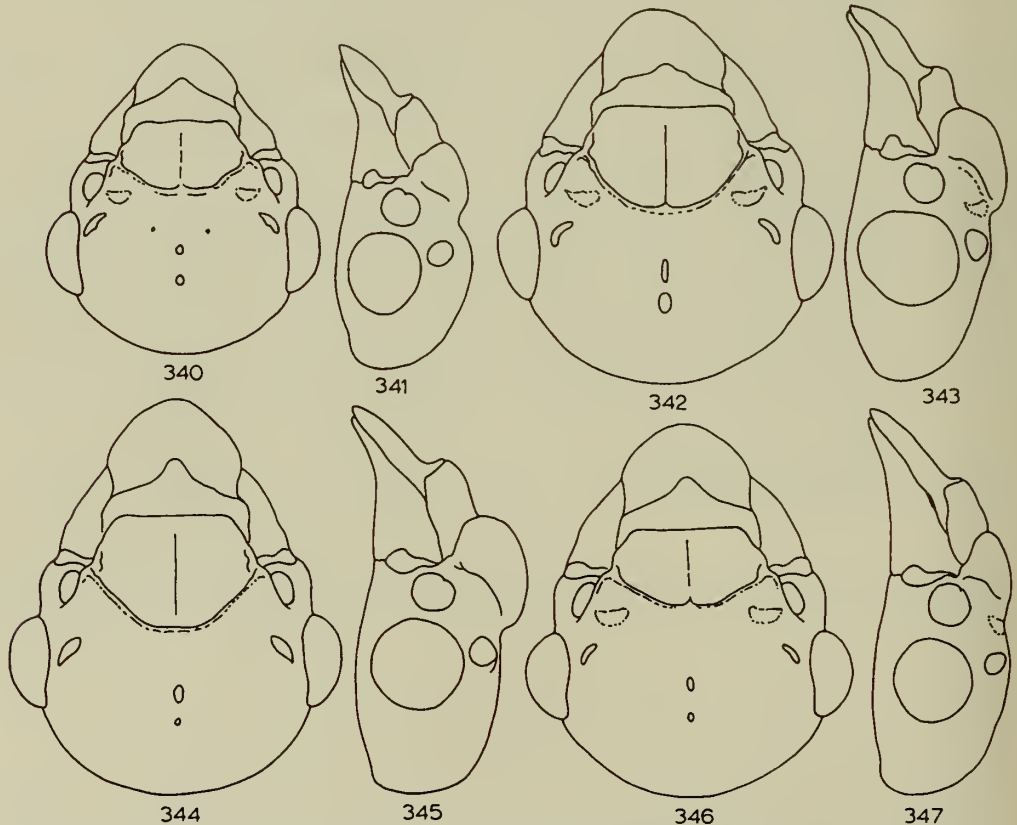
	Range	Mean
Head width across eyes (W)	0.98-1.06	1.015
Ocellus ($O_w \times O_1$)	0.08-0.09 \times 0.10-0.11	0.080 \times 0.106
Ocellus to eye (O-E)	0.04-0.06	0.048
Postclypeus length (Pcl)	0.30-0.35	0.321
Antennal article III	0.03-0.04	0.030
Antennal article IV	—	0.047
Antennal article V	—	0.051
Left mandible, apical to first marginal (L_A)	0.11-0.12	0.111
Left mandible, first to third marginal (L_1)	0.15-0.16	0.156
Left mandible, third marginal to molar (L_m)	—	0.060
Right mandible, apical to first marginal (R_A)	0.10-0.12	0.110
Right mandible, first to second marginal (R_1)	0.11-0.12	0.113
Right mandible, second marginal to molar (R_m)	0.06-0.07	0.066
Mesonotum width (M)	0.24-0.29	0.271
Metanotum width (N)	0.23-0.30	0.272

Worker. Head capsule and pilosity pale yellow, setae sparse. Postclypeus strongly inflated, Pcl/W, 0.33-0.35. Apical teeth of mandibles long, L_A/L_1 , 0.81-0.82, R_A/R_1 , 0.97-1.00; subsidiary marginal tooth of left mandible well clear of molar prominence, separated from it by distinct notch in surface view, $L_A/L_1.L_m$, 20.75-21.20; anterior edges of first and second marginal teeth subequal, $R_A/R_1.R_m$, 22.80. Fore tibia scarcely swollen. T_1/T_w , 5.25-5.30, third spur vestigial, one-quarter or less of length of other two. Mesenteric overlap with proctodeum approximately twice as long as width of mesenteron at insertion of malpighian tubules, anterior end of proctodeum touching malpighian knot; enteric valve seating dorsolateral in unopened abdomen; internal cushions of enteric valve all equally fairly distinctly developed, with scaly surface, posterior margin of each scale bearing one small point or spine. Membranous wall of valve beyond cushions with numerous minute spicules tending to be arranged in rows. Other characters in generic diagnosis.

Measurements (two specimens from two localities) in millimetres:

Head width (W)	0.73-0.76
Fore tibia width (T_w)	0.10-0.11
Fore tibia length (T_l)	0.53-0.56
Postclypeus length (Pcl)	0.25
Left mandible, apical to first marginal (L_A)	0.09
Left mandible, first to third marginal (L_1)	0.11
Left mandible, third marginal to molar (L_m)	0.04
Right mandible, apical to first marginal (R_A)	0.09
Right mandible, first to second marginal (R_1)	0.09
Right mandible, second marginal to molar (R_m)	0.04

A. epius has already been compared with *A. chirotus* in the discussion on that species. It is about the same size as *A. tithasus*, but has a much more inflated postclypeus in both imago and worker castes, and the ocelli are closer to the compound eyes. *A. epius* is the only species of the genus which in the worker has a mesenteric overlap with the proctodeum, and a vestigial third apical spur on the slender fore tibia. There is a little doubt about this character in the imago, since although the third spur is vestigial in the type-series, it is fully developed in another



FIGS 340-347. *Acholotermes*, imago head capsules, front and side views. 340, 341, *A. chirotus*; 342, 343, *A. epius*; 344, 345, *A. imbellis*; 346, 347, *A. tithasus*.

imago pair that appear conspecific. *A. imbellis* is distinguished in the imago by the minute fontanelle, longer apical mandibular teeth, and wider meso- and metanota. The worker differs from *A. epius* in the characters already mentioned above. The abdomen appears to be possibly dehiscent in the worker caste of *A. epius*, but this is not very definite.

Holotype ♀ imago, paratype ♂ and ♀ imagos and workers from type-colony, ZAMBIA: Lusaka, 11.xii.1966 (*M. G. Bingham*, Coll. No. 553) in British Museum (Natural History).

Other paratype material. RHODESIA: Salisbury, Atlantika Research Station, 19.xii.1964 (*M. G. Bingham*, Coll. No. 158), in BMNH.

The species was found in mounds of *Cubitermes* spp.



FIGS 348-355. *Acholotermes*, imago mandibles. 348, 349, *A. chivotus*; 350, 351, *A. epius*; 352, 353, *A. imbellis*; 354, 355, *A. tithasus*.

Acholotermes imbellis sp. n.

(Text-figs 344, 345, 352, 353 & 368-373; Pl. 3, fig. 4)

Imago. Head capsule sepia-brown, darker above ocelli; fontanelle vestigial, minute, circular, flat or very slightly depressed and coloured as head; medial spot oval, slightly raised, larger than fontanelle, also coloured as head; postclypeus brown, labrum pale yellow-brown; frontal marks small, flat, semicircular, sepia-brown; antennae yellow-brown. Pronotum, meso- and metanota brown, transverse dark sutures present; femora yellow-brown, tibiae paler, tarsi yellow. Abdominal tergites brown, dorsal stigmata sepia-brown, sternites yellow-brown, paler in middle, ventral stigmata brown; cerci yellow.

Posterior margin of head capsule evenly rounded; ocelli medium-sized, separated from compound eyes by less than half own least diameter; postclypeus strongly inflated, Pcl/W, 0.32-0.34, posterior margin bowed, not evenly rounded, median suture present, weak anteriorly. Apical teeth of mandibles long, L_A/L_1 , 0.89-0.91, R_A/R_1 , 1.13-1.24; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 12.67-14.22; point of first marginal tooth of left mandible slightly behind line of apical to second marginal, anterior edges of first and second marginals approximately equal. Pilosity of head capsule uneven, not forming a pelt, brown. Meso- and metanota fairly wide at constriction. M/W, 0.30-0.31. Fore tibia with third apical spur distinct, about two-thirds length of other two.

Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	0.97-1.06
Ocellus ($O_w \times O_l$)	0.08-0.09 \times 0.10-0.11
Ocellus to eye (O-E)	0.04
Postclypeus length (Pcl)	0.31-0.36
Antennal article III	0.02-0.03
Antennal article IV	0.03-0.04
Antennal article V	0.05
Left mandible, apical to first marginal (L_A)	0.13
Left mandible, first to third marginal (L_1)	0.14
Left mandible, third marginal to molar (L_m)	0.06-0.07
Right mandible, apical to first marginal (R_A)	0.13
Right mandible, first to second marginal (R_1)	0.10-0.11
Right mandible, second marginal to molar (R_m)	0.06-0.07
Mesonotum width (M)	0.29-0.33
Metanotum width (N)	0.30-0.35

Worker. Head capsule pale yellow, pilosity yellow, rather dense on both head and body. Postclypeus strongly inflated, Pcl/W, 0.33. Apical teeth of mandibles very long, L_A/L_1 , 1.00, R_A/R_1 , 1.18; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, $L_A/L_1.L_m$, 22.89; anterior edges of first and second marginal teeth of right mandible approximately equal, $R_A/R_1.R_m$, 23.50. Fore tibia weakly swollen, T_1/T_w , 4.27, third apical spur distinct, about half length of other two. Mesenteric junction with proctodeum angled between transverse and diagonal, touching malpighian knot; enteric valve seating lateral in unopened abdomen; internal cushions of enteric valve moderately developed, with scaly

surface, posterior margin of each scale fringed with minute spicules. Membranous wall of valve beyond cushions with very numerous fine small spicules arranged in 15–20 rows, broken up into fringed lobes, between cushions. Other characters in generic diagnosis.

Measurements (one specimen) in millimetres.

Head width (W)	0.80
Fore tibia width (T_w)	0.14
Fore tibia length (T_1)	0.59
Postclypeus length (Pcl)	0.26
Left mandible, apical to first marginal (L_A)	0.11
Left mandible, first to third marginal (L_1)	0.11
Left mandible, third marginal to molar (L_m)	0.04
Right mandible, apical to first marginal (R_A)	0.11
Right mandible, first to second marginal (R_1)	0.09
Right mandible, second marginal to molar (R_m)	0.05

A. imbellis has already been compared with *A. chirotus* and *A. epius* under those species. It is distinguished from *A. tithasus* in both imago and worker castes by its much more strongly inflated postclypeus, and in the imago by the ocelli being much closer to the eyes. In the worker caste, *A. tithasus* also has noticeably bristly fore coxae in contrast to *A. imbellis*. The abdomen of the worker caste appears to be dehiscent in this species.

Holotype queen, paratype king, and workers from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Katanga, Keyberg, near Elizabethville, 21.V.1948 (*A. E. Emerson*), in American Museum of Natural History.

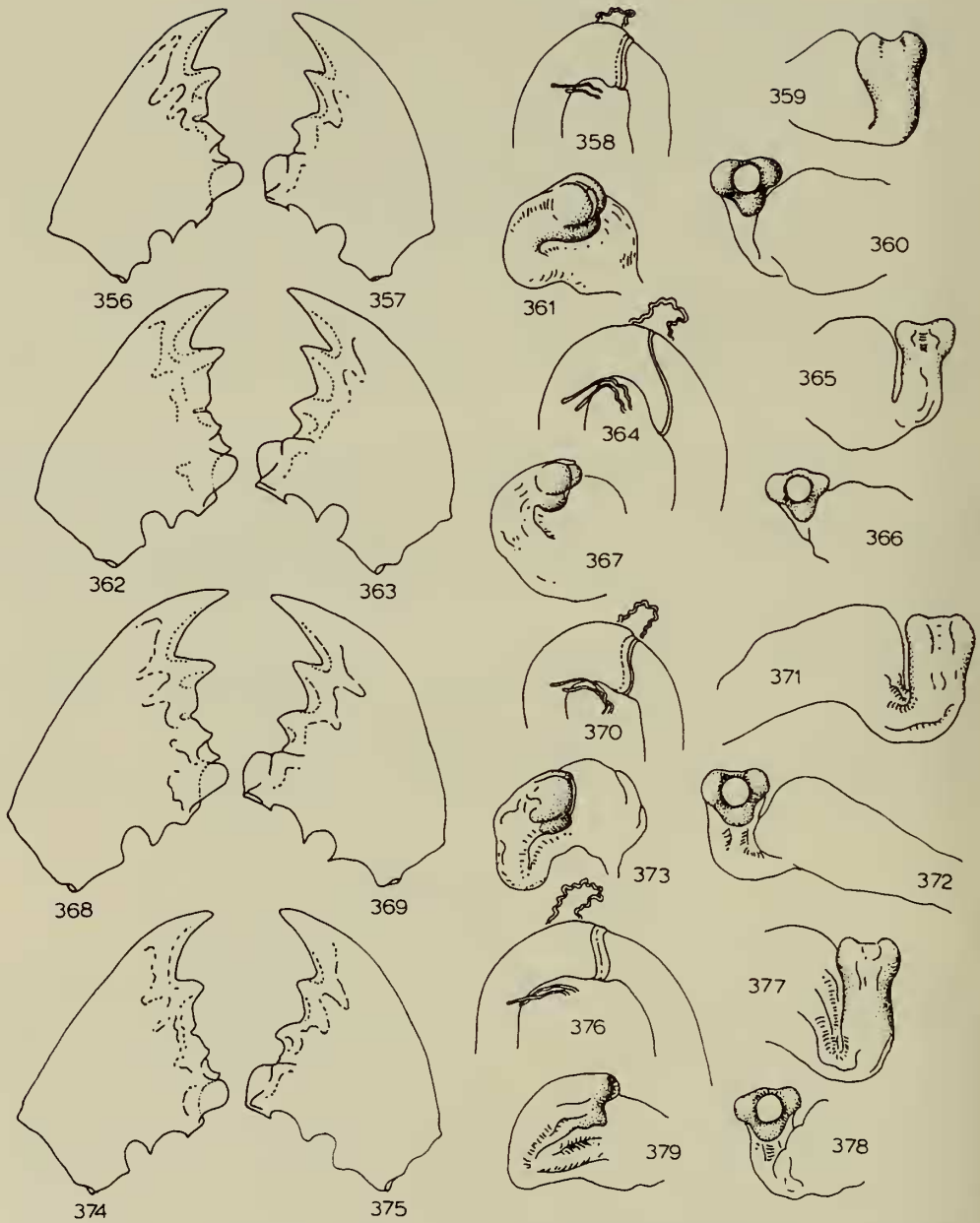
The single known nest-series was found near the surface of an old mound, probably of *Cubitermes* sp., in grassy woods near the top of a rocky hillside.

Acholotermes tithasus sp. n.

(Text-figs 346, 347, 354, 355 & 374–379; Pl. 3, figs 5 & 6)

Imago. Head capsule sepia-brown, darker above ocelli; fontanelle small, circular, flat, less than one-fifth size of ocellus, pale brown; medial spot twice as large as fontanelle, flat, coloured as head; postclypeus sepia-brown, labrum yellow-brown; frontal marks flat crescents, coloured as head; antennae brown. Pronotum sepia-brown, meso- and metanota brown, transverse dark sutures absent from mesonotum, weakly present on metanotum; femora and tibiae pale yellow-brown, tarsi yellow. Abdominal tergites brown, dorsal stigmata paler, sternites yellow-brown laterally with paler ventral stigmata, yellow in middle; cerci yellow.

Posterior margin of head capsule slightly arched, not evenly rounded; ocelli rather small, separated from compound eyes by slightly more than own least diameter; postclypeus weakly inflated, Pcl/W, 0.23, posterior margin almost obtusely angular, not evenly rounded, median suture weak. Apical teeth of mandibles very long, L_A/L_1 , 0.91–1.04, R_A/R_1 , 1.33–1.45; subsidiary marginal tooth of left mandible level with edge of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 13.50–16.29; point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edges of first tooth and second marginals equal.



FIGS 356-379. *Acholotermes*, worker mandibles, mesenteric-proctodeal junctions showing attachments of malpighian tubules and positions of malpighian knot, and views of enteric valve seatings. 356-361, *A. chirotus*; 362-367, *A. epius*; 368-373, *A. imbellis*; 374-379, *A. tithasus* (mandibles somewhat worn).

Pilosity of head capsule uneven, not forming a pelt. Meso- and metanota fairly wide at constriction, M/W, 0.30-0.32. Fore tibia with third apical spur nearly as long as other two.

Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	0.99-1.03
Ocellus ($O_w \times O_l$)	0.07 \times 0.09
Ocellus to eye (O-E)	0.06-0.07
Postclypeus length (Pcl)	0.25-0.24
Antennal article III	0.05-0.06
Antennal article IV	0.05
Antennal article V	0.05
Left mandible, apical to first marginal (L_A)	0.14-0.15
Left mandible, first to third marginal (L_1)	0.14-0.15
Left mandible, third marginal to molar (L_m)	0.06-0.07
Right mandible, apical to first marginal (R_A)	0.15
Right mandible, first to second marginal (R_1)	0.10-0.11
Right mandible, second marginal to molar (R_m)	0.06-0.08
Mesonotum width (M)	0.31
Metanotum width (N)	0.33-0.35

Worker. Head capsule and pilosity yellow. Postclypeus moderately inflated, Pcl/W, 0.28. Apical teeth of mandibles very long, L_A/L_1 , 1.07, R_A/R_1 , 1.29; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, $L_A/L_1.L_m$, 22.55; anterior edge of first marginal tooth of right mandible shorter than that of second, $R_A/R_1.R_m$, 30.15. Fore tibia moderately swollen, T_1/T_w , 3.92, third apical spur about two-thirds length of other two. Mesenteric junction with proctodeum transverse, to right of malpighian knot; enteric valve-seating lateral or slightly dorsolateral in unopened abdomen; internal cushions of enteric valve moderately developed, with scaly surface, posterior margin of each scale fringed with several small spines. Membranous wall of valve beyond cushions with very numerous fine but distinct spicules arranged in 15-20 rows, only slightly broken into fringed lobes between posterior ends of cushions. Other characters in generic diagnosis.

Measurements (one specimen) in millimetres.

Head width (W)	0.80
Fore tibia width (T_w)	0.15
Fore tibia length (T_1)	0.59
Postclypeus length (Pcl)	0.23
Left mandible, apical to first marginal (L_A)	0.11
Left mandible, first to third marginal (L_1)	0.11
Left mandible, third marginal to molar (L_m)	0.05
Right mandible, apical to first marginal (R_A)	0.11
Right mandible, first to second marginal (R_1)	0.09
Right mandible, second marginal to molar (R_m)	0.04

The comparisons of this, the type-species, with the remaining members of the genus, have already been made under their individual headings. The abdomen seems to be weakly dehiscent in the worker caste of *A. tithasus*.

Holotype ♀ imago, paratype ♂ and ♀ imagos and workers from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Yangambi, 29.v.1948 (*A. E. Emerson*), in American Museum of Natural History. (Paratypes from type-colony, ♀ and ♂ imagos and workers, also in BMNH.)

The single known nest-series was found in a mound 5 ft in diameter, 3 ft high, at the base of a tree.

AMICOTERMES gen. n.

(Amicus, L., 'friend(ly), kind')

Type-species: *Amicotermes galenus* sp. n.

Imago. Medium-sized, W, 1.01. Compound eyes proportionately rather small, W/E, 4.5 (all other genera and species under 4.2, most under 4.0). Fore tibia with three apical spurs, third very small, almost vestigial; fore coxae thickly setose, somewhat spiny on anterior edge. Apical teeth of mandibles very long, L_A/L_1 , 0.99. R_A/R_1 , 1.36; subsidiary marginal tooth of right mandible with proximal end just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 14.08. Point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edges of first and second marginals subequal. Meso- and metanota rather narrow at constriction, M/W, 0.28, transverse dark sutures absent; complex ratio of mandible and notal measurements, $L_1/M.N$, 1.60.

Worker. Medium-sized, W, 0.76. Fore tibia weakly swollen, T_1/T_w , 4.32, with three apical spurs, third spur small, about one-third other two; fore coxae and rest of leg strongly setose, bristly, apex of tibia and base of femur with opposing interlocking bristles when folded (only genus in which this is found). Apical teeth of mandibles very long, L_A/L_1 , 1.09, R_A/R_1 , 1.33; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio $L_A/L_1.L_m$, 26.50; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edges of first and second marginals subequal, complex ratio, $R_A/R_1.R_m$, 31.25. Mesenteric junction with proctodeum nearly transverse, slightly angled, to right of malpighian knot. Enteric valve seating definitely three-lobed, third lobe only slightly smaller than outer two, connected to second pouch of proctodeum by very long neck, lateral in position in unopened abdomen; internal cushions of enteric valve produced through valve opening, those in position 3 slightly more elongated than the others, all positions armed in posterior one-third of length with numerous irregularly arranged elongated spines; rest of cushion surface scaly, most scales edged with small or minute spines. Membranous wall of valve beyond cushions with numerous fine but pronounced spicules, between cushions with numerous spicule-fringed carunculations.

Amicotermes was at first grouped with *Acholotermes* on the basis of the similarity of the imago and worker mandibles, and the layout of the worker gut. However, the worker enteric valve-armature is much more developed, and the imago rather different in appearance with its unusually small compound eyes. The spiny or setose coxae of worker and imago are another unusual feature supporting the placement of the single species in a monotypic genus. The vector and cluster analyses of the similarity matrix also separate it widely from *Acholotermes*. The enteric valve armature of *Amicotermes* is superficially similar to that of *Apagotermes*, but in the latter genus the imago and worker mandibles are quite different, and the valve

armature consists of regularly arranged spines, those below the outermost row being slightly spatulate. In the cluster analysis *Amicotermes* is placed near *Aderitotermes*. This genus, however, has a long mixed segment and distinctive enteric valve-armature in the worker caste, shorter mandibular apical teeth in both castes, and regular pilosity forming a pelt on the head capsule of the imago. *Adynatotermes* has similarly long apical teeth but is otherwise very different, not least in size.

Since the decision to separate *Amicotermes* as a monotypic genus was taken a second species has been discovered in West Africa. This is known only from the worker caste, and is therefore not described here, as in other genera where the same thing has happened. The occurrence of these extra species in monotypic or small genera is interesting because they strengthen the conviction that the generic groupings used here will form a valid and stable basis for their future classification.

Amicotermes galenus sp. n.

(Text-figs 380-389; Pl. 3, figs 7-10)

Imago. (Queen, colours possibly faded.) Head capsule sepia-brown, darker above ocelli; fontanelle flat, short oval, pale yellow, about half size of ocellus; medial spot circular, flat, slightly smaller than fontanelle, coloured as head; postclypeus brown, labrum yellow; frontal marks semicircular, flat, brown; antennae pale yellow-brown. Pronotum brown, meso- and metanota yellow-brown, femora and tibiae yellow, tarsi paler. Abdominal tergites yellow-brown, dorsal stigmata paler, sternites pale yellow-brown, ventral stigmata and middle sternites paler; cerci yellow.

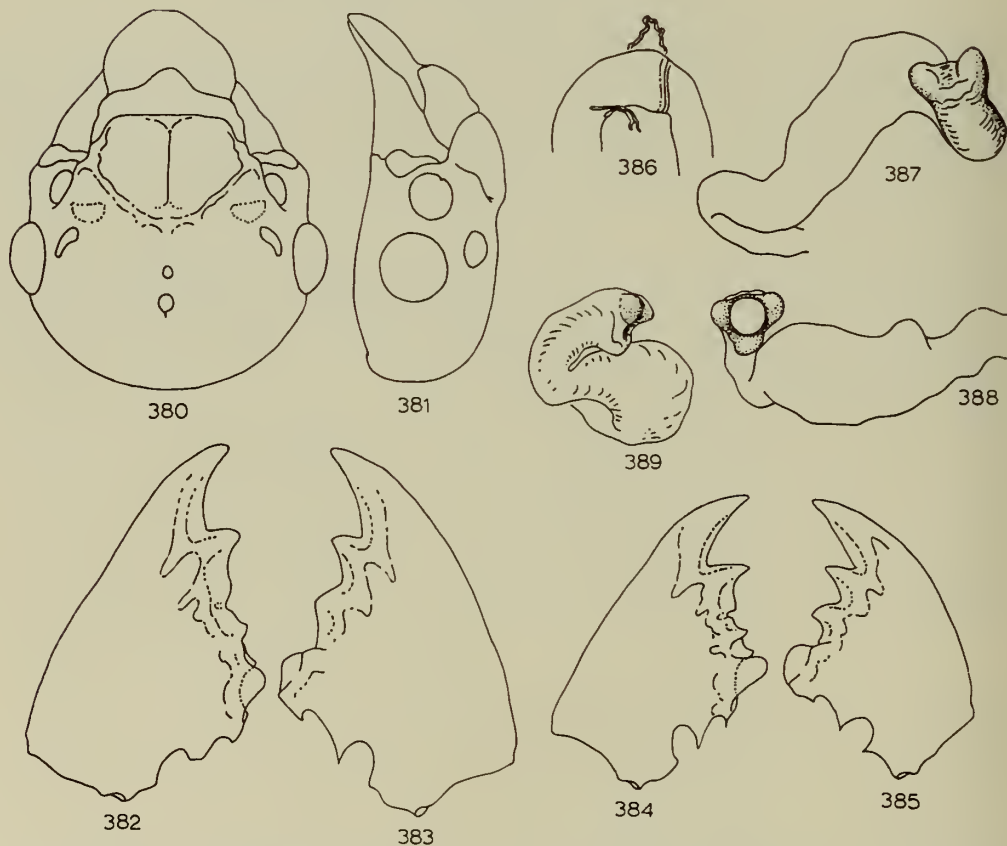
Posterior margin of head capsule evenly rounded; ocelli medium-sized, separated from compound eyes by somewhat less than own least diameter; postclypeus strongly inflated, Pcl/W, 0.33, posterior margin rather angularly arched, median suture distinct. Pilosity of head capsule very dense, yellow-brown, somewhat uneven, almost forming a pelt but obscured by many emergent setae. Other characters in generic diagnosis.

Measurements (one specimen) in millimetres.

Head width across eyes (W)	1.01
Ocellus ($O_w \times O_l$)	0.09 \times 0.12
Ocellus to eye (O-E)	0.07
Postclypeus length (Pcl)	0.34
Antennal article III	0.04
Antennal article IV	0.05
Antennal article V	0.05
Left mandible, apical to first marginal (L_A)	0.14
Left mandible, first to third marginal (L_1)	0.14
Left mandible, third marginal to molar (L_m)	0.07
Right mandible, apical to first marginal (R_A)	0.14
Right mandible, first to second marginal (R_1)	0.10
Right mandible, second marginal to molar (R_m)	0.07
Mesonotum width (M)	0.29
Metanotum width (N)	0.30

Worker. Head capsule and pilosity yellow, setae rather sparse, not conspicuous. Postclypeus strongly inflated, Pcl/W , 0.33, Pcl/R_1 , 3.28. Other characters given in generic diagnosis. Measurements (one specimen) in millimetres.

Head width (W)	0.76
Fore tibia width (T_w)	0.13
Fore tibia length (T_1)	0.56
Postclypeus length (Pcl)	0.25
Left mandible, apical to first marginal (L_A)	0.10
Left mandible, first to third marginal (L_1)	0.10
Left mandible, third marginal to molar (L_m)	0.04
Right mandible, apical to first marginal (R_A)	0.10
Right mandible, first to second marginal (R_1)	0.08
Right mandible, second marginal to molar (R_m)	0.04



FIGS 380-389. *Amicotermes galenus*. 380, 381, front and side views of imago head capsule; 382, 383, imago mandibles; 384, 385, worker ditto; 386, mesenteric-proctodeal junction showing attachments of malpighian tubules and position of malpighian knot; 387-389, views of enteric valve seating.

The distinguishing features of this species are discussed under the generic headings. It remains only to note that the abdomen of the worker caste appears to be dehiscent in *A. galenus*.

Holotype ♀ imago (queen) and paratype workers from type-colony only, DEMOCRATIC REPUBLIC OF CONGO: Katanga, Keyberg, near Elizabethville, 21.v.1948 (*A. E. Emerson*) in American Museum of Natural History.

The single nest-series of this species, like that of *Acholotermes imbellis*, was found in an old mound, probably of *Cubitermes*, on a rocky hillside in grassy woodland.

APAGOTERMES gen. n.

(Apages, Gr., 'soft, weak')

Type-species: *Apagotermes stolidus* sp. n.

Imago. Small-sized, W, 0.74. Fore tibia with three apical spurs, third nearly equal in size to other two. Apical teeth of mandibles short, L_A/L_1 , 0.55, R_A/R_1 , 0.67-0.71; subsidiary marginal tooth of left mandible with proximal end just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 9.09-9.50; points of apical and marginal teeth of right mandible nearly in line, anterior edge of first marginal shorter than that of second, the latter curved. Meso- and metanota narrow at constriction, M/W, 0.21, transverse dark sutures present, weak on mesonotum; complex ratio of mandible and notal measurements, $L_1/M.N$, 4.36-4.70.

Worker. Very small, W, 0.58. Fore tibia moderately swollen, T_1/T_w , 3.84 with three apical spurs, third about half other two. Apical teeth of mandibles short, L_A/L_1 , 0.52, R_A/R_1 , 0.67; subsidiary marginal tooth of left mandible with proximal end level with edge of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 12.70; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal shorter than that of second, complex ratio, $R_A/R_1.R_m$, 15.80. Mesenteric junction with proctodeum very nearly transverse, to right of malpighian knot. Enteric valve-seating weakly three-lobed, two outer lobes tending to be opposite, but no longer than third, connected to second pouch of proctodeum by distinct but very short neck, dorsolateral in position in unopened abdomen; internal cushions of enteric valve all equally produced through valve opening; all positions armed in posterior one-third of length with regularly arranged rows of elongated spines, those below outermost row somewhat spatulate or ensiform, alternate cushions, i.e., positions 1 and 3, with slightly fewer spines; rest of cushion surface with small or minute spines.

The small size of *Apagotermes* distinguishes it from many other genera including the previous genus, *Amicotermes* in which the worker enteric valve is superficially similar. Other distinguishing features are given under that genus. The imago of *Astalotermes obstructus* resembles *Apagotermes* but has a somewhat longer postclypeus, wider meso- and metanota, and ocelli closer to the eyes. The workers are easily distinguished by the gut characters. *Astalotermes benignus* has a similar size range, but the vestigial third tibial spur is diagnostic. In the smaller *Astalotermes* species, there seems to be less discrepancy in size between imago and worker castes than there is in *Apagotermes*. *Astalotermes comis* is again about the same size but the mandibular teeth are very differently proportioned and the postclypeus more inflated.

Apagotermes is one of the most isolated genera and species in the cluster analyses of the similarity matrix. It is the last to join in the single linkage, and penultimate

in the median sorting. In the vector analyses it seems not so much an outlier as a genus which is isolated by falling in a 'gap' in the hyperspace. It has an unusual combination of values for the first five or six principal co-ordinates, although no individual value in any vector approaches the extremes.

Apagotermes stolidus sp. n.

(Text-figs 390-399; Pl. 4, figs 1 & 2)

Imago. Head capsule sepia-brown, darker above ocelli, fontanelle very small, almost vestigial, elongate oval, very slightly raised, brown; medial spot elongate oval, equal to fontanelle or slightly smaller, raised on small bump, coloured as head; postclypeus brown, labrum pale yellow-brown; frontal marks weakly developed, rather indistinct, flat brown crescents; antennae yellow-brown. Pronotum brown, meso- and metanota yellow-brown; femora pale yellow-brown, tibiae and tarsi yellow. Abdominal tergites brown, dorsal stigmata paler, sternites and ventral stigmata pale brown; middles of sternites and cerci yellow.

Posterior margin of head capsule slightly undulating, not evenly rounded; ocelli moderately large, separated from compound eyes by about two-fifths own least diameter; postclypeus very weakly inflated, Pcl/W, 0.21, posterior margin indistinctly arched, median suture absent. Pilosity of head capsule dense, somewhat uneven but almost forming a rough pelt with numerous irregular emergent setae. Other characters in generic diagnosis.

Measurements (two specimens, one locality) in millimetres.

Head width across eyes (W)	0.74
Ocellus ($O_w \times O_l$)	0.07 × 0.09
Ocellus to eye (O-E)	0.03
Postclypeus length (Pcl)	0.15-0.16
Antennal article III	0.02
Antennal article IV	0.03-0.04
Antennal article V	0.04
Left mandible, apical to first marginal (L_A)	0.06-0.07
Left mandible, first to third marginal (L_1)	0.12
Left mandible, third marginal to molar (L_m)	0.06
Right mandible, apical to first marginal (R_A)	0.07
Right mandible, first to second marginal (R_1)	0.09-0.10
Right mandible, second marginal to molar (R_m)	0.05-0.06
Mesonotum width (M)	0.16
Metanotum width (N)	0.16-0.17

Worker. Head capsule yellow, pilosity orange-yellow, fairly numerous but not dense, short, not conspicuous. Postclypeus weakly inflated, Pcl/W, 0.25, Pcl/ R_1 , 1.80. Other characters given in generic diagnosis.

Measurements (one specimen) in millimetres.

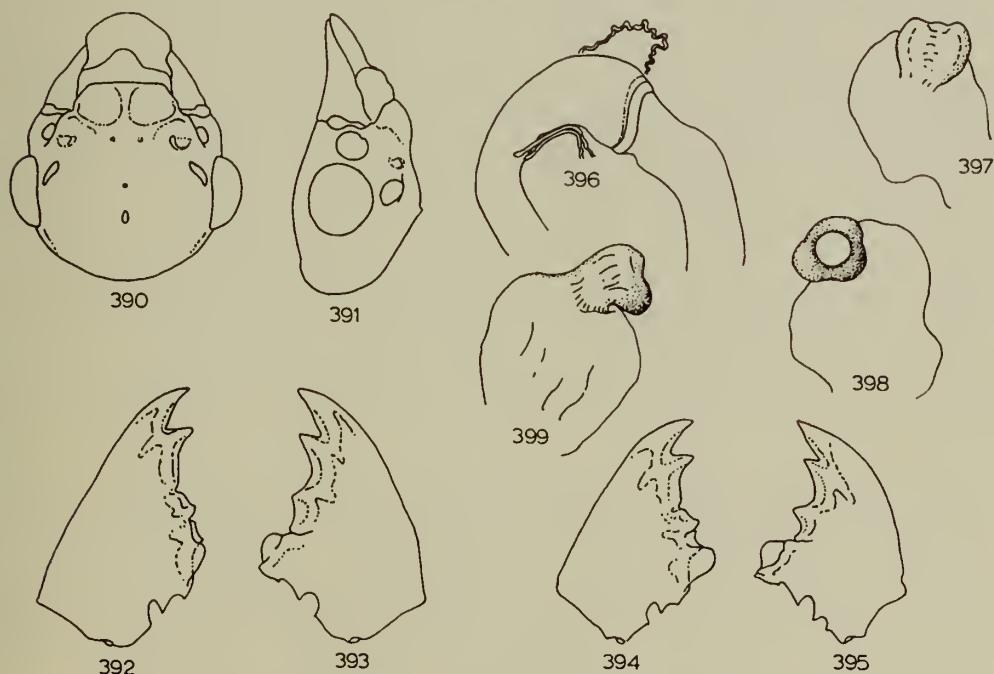
Head width (W)	0.58
Fore tibia width (T_w)	0.10
Fore tibia length (T_1)	0.38
Postclypeus length (Pcl)	0.14

Left mandible, apical to first marginal (L_A)	0.05
Left mandible, first to third marginal (L_1)	0.10
Left mandible, third marginal to molar (L_m)	0.04
Right mandible, apical to first marginal (R_A)	0.05
Right mandible, first to second marginal (R_1)	0.08
Right mandible, second marginal to molar (R_m)	0.04

The comparisons of *A. stolidus* with other species and genera having been made under the generic heading, it remains to add that the abdomen of the worker caste has at least a tendency to be dehiscent.

Holotype ♀ imago, paratype ♂ and ♀ imagos and workers from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Epulu River, Camp Putnam, 12.v.1948 (*A. E. Emerson*, Coll. No. 18) in American Museum of Natural History. (Other paratype ♂ and ♀ imago and workers from type-colony in BMNH.)

Other paratype material. NIGERIA: Eastern Region (*W. Wilkinson*) in British



FIGS 390-399. *Apogotermes stolidus*. 390, 391, front and side views of imago head capsule; 392, 393, imago mandibles; 394, 395, worker ditto; 396, mesenteric-proctodeal junction showing attachment of malpighian tubules and position of malpighian knot; 397-399, views of enteric valve seating.

Museum (Natural History). DEMOCRATIC REPUBLIC OF CONGO: Kivu, Irangi, 2.xi.1963 (*E. Ernst*) Swiss Tropical Institute, Basle and BMNH.

The type-series was found in the top 3-4 inches of soil on a mound of *Protermes prorepens* (Macrotermitinae) in rain forest.

ATEUCHOTERMES gen. n.

(Ateuches, Gr., 'unarmed')

Type-species: *Ateuchotermes pectinatus* sp. n.

Imago. Medium-sized to large, W, 0.90-1.30. Fore tibia with three apical spurs, third well developed, one-third or more length of other two, except in one species in which it is vestigial. Apical teeth of mandibles short or fairly short, L_A/L_1 , 0.50-0.66, R_A/R_1 , 0.66-1.01; subsidiary marginal tooth of left mandible with proximal end just clear to widely clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 5.33-9.10; points of apical and marginal teeth of right mandible in line, or first marginal retracted slightly behind line of apical to second marginal, anterior edge of first marginal equal to that of second, or longer. Meso- and metanota rather narrow to distinctly wider at constriction, M/W , 0.26-0.34, transverse dark sutures weak or absent on mesonotum in most species, only distinct in one, present or absent on metanotum; complex ratio of mandible and notal measurements, $L_1/M.N$, 1.07-1.92.

Worker. Medium sized to very large, W, 0.75-1.10. Fore tibia scarcely swollen or slender. T_1/T_w , 4.72-5.90, with three apical spurs, third small or vestigial, maximum about one-third of other two. Apical teeth of mandibles short to moderately long, L_A/L_1 , 0.45-0.74, R_A/R_1 , 0.59-1.01; subsidiary marginal tooth of left mandible with proximal end level with edge of molar prominence (one species only) or distinctly clear of it in surface view, complex ratio, $L_A/L_1.L_m$, 8.32-14.41; points of apical and marginal teeth of right mandible more or less in line, or first marginal distinctly retracted behind line of apical to second marginal, anterior edge of first marginal equal to that of second or markedly shorter, complex ratio, $R_A/R_1.R_m$, 10.40-17.10. Mesenteric junction with proctodeum diagonal or a little longer, to right of malpighian knot. Enteric valve-seating rather large, weakly two-lobed, sessile on second pouch of proctodeum or connected to it by short neck, dorsolateral to dorsal in unopened abdomen; internal cushions of enteric valve all sclerotized and produced through valve opening, that in position 1 enlarged, elongated, and dilated at its posterior end which curves out into enteric valve seating; armature in position 1 numerous elongated spines in comb- or rake-like formation in one or more rows round rim; armature in positions 2, 3 and 4 elongated, more slender spines, sometimes hooked at tips, fewer in number than position 1, in fork-like formation at posterior ends of cushions; all cushions sometimes with small spines on remainder of length or without further armature.

The enteric valve armature of the worker caste of *Ateuchotermes* is the most complex in the entire group and the most easily recognized. The function of this fantastic structure can only be a source of speculation. The cushion in position 1 has elongated to an extent where it hooks out of the enteric valve itself into its seating. Its spines touch the wall of the seating, where in one species a sclerotized cup has developed to receive them. The teeth of this structure are too far out to act as a filter. Only two possibilities suggest themselves. It could hold a colony of symbiotic bacteria against the wall of the gut and prevent their dispersion; or it could form a springy linking device to prevent the enteric valve pulling out of its seating. This in some other genera it seems to do very easily, in preserved material, being almost impossible to keep in place in dissections. It may be envisaged that

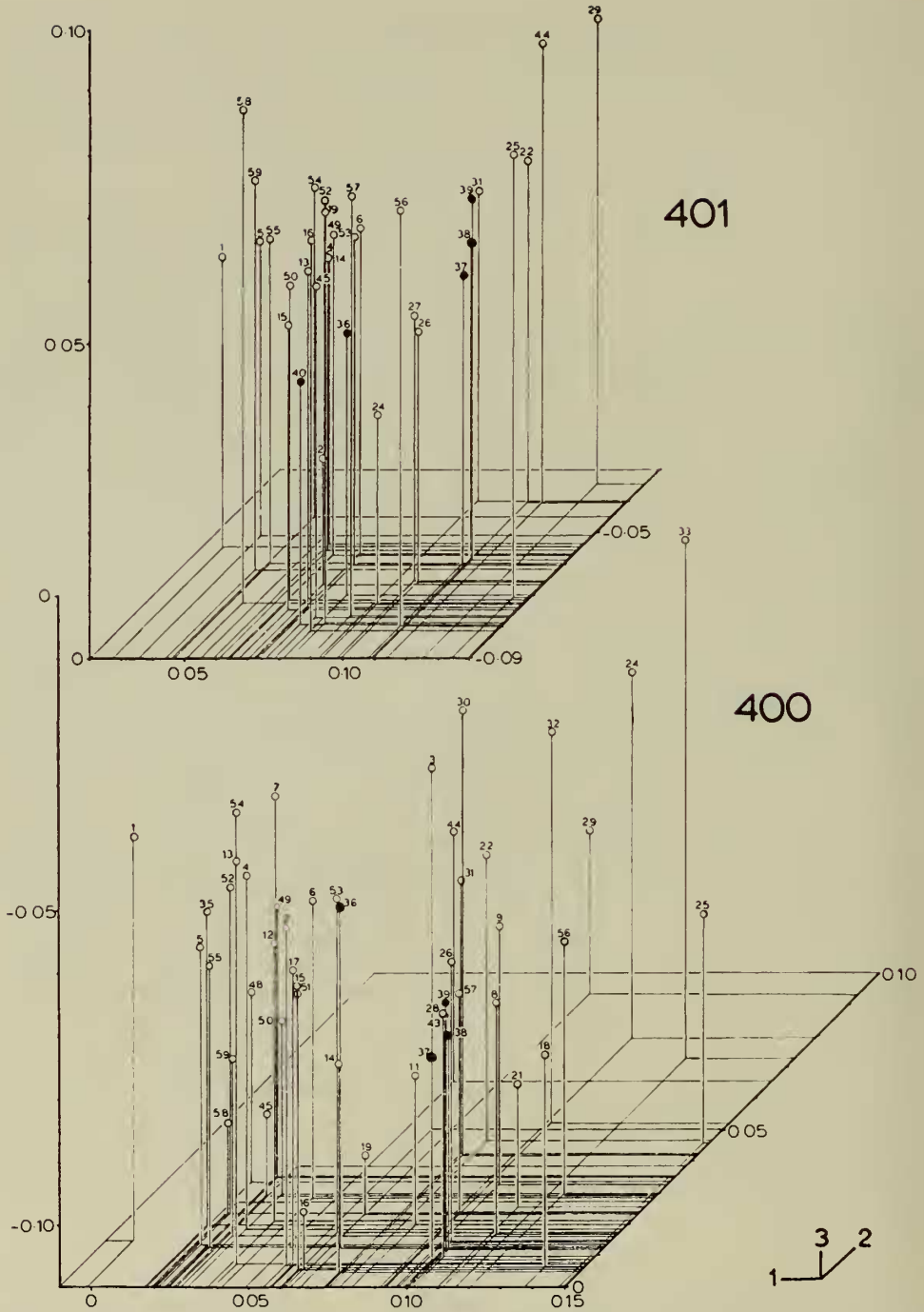
an easily ruptured gut might be an advantageous adjunct of a dehiscent abdomen as a suicidal defence mechanism. The abdomen certainly appears to be dehiscent to a very marked extent in all species of *Ateuchotermes*. However, in the narrow tunnels and crannies of their habitat the muscular contortions of their movements might set off the mechanism prematurely, and it could well be that this development took place to counteract the over-developed suicidal tendency. The connection would also tend to rupture more abruptly under the hydrostatic pressure, resulting in a more effective defensive explosion. Whatever its function, this structure provides a set of extremely valuable taxonomic characters. The spines on cushions in positions 2, 3 and 4 are clearly a development of the simple backwardly directed non-return mechanism seen in many other genera. In some species they appear to be capable of forming a filtering network held together by hooks at their tips. Within the genus *Ateuchotermes* these structures form a sequence of developing elaboration. A further species is known in which all cushion positions are developed to about the same extent, and like positions 2, 3 and 4. This would seem to indicate a relationship with other genera such as *Apagotermes* and possibly *Amicotermes*. The enteric valve of this species is included in the illustrations of the genus to show the relationship, but since only the worker caste is available it is not described or included in keys (Pl. 4, figs 3 & 4).

Ateuchotermes is one of the more compact and well-defined genera in the cluster and vector analyses (Text-fig. 402) of the similarity matrix. In both single linkage and median sorting the group forms above the 80% phenon level, 86% in the case of single linkage and joins with related groups at the 75-78% level. Genera placed close to *Ateuchotermes* in some eigenvectors of the principal co-ordinates analysis, as well as the cluster analyses, are *Alyscotermes*, *Anaorotermes*, *Acholotermes*, *Amicotermes* and *Aderitotermes*. Because the enteric valve of *Ateuchotermes* workers is so distinctive, there is no need to compare this caste to related genera. In the imago, *Alyscotermes* is distinguished by its rather regularly oval fontanelle; in *Ateuchotermes* this is never very clearly defined, and if nearly oval, is very small and indistinct. *Anaorotermes*, *Acholotermes* and *Amicotermes* have uneven pilosity, and the two latter genera, longer apical mandibular teeth. *Aderitotermes* has a sharply defined, pale coloured fontanelle. One species of *Ateuchotermes* keys out next to *Adynatotermes* but is smaller with larger eyes and ocelli and less inflated postclypeus. Certain species of *Astratotermes*, in particular *A. pacatus*, are very difficult to distinguish from one or two *Ateuchotermes* in which the fontanelle approaches oval shape. In *A. pacatus* the outline of the fontanelle has a tendency to be indistinct in some specimens, and there is no other character that can be used to separate it in the imago. Measurement characters provided no clear generic discrimination in either caste as shown by the canonical variates analyses in Text-figs 400 & 401.

KEY TO SPECIES

Imagos

- 1 Compound eyes and ocelli large, W/E, 3.26-3.58, O_w/O-E, 2.27-5.60 (i.e. separated by less than half least diameter of ocellus) 2



FIGS 400 & 401. Three-dimensional graphs of canonical variates 1, 2 & 3 showing species of *Ateuchotermes* as solid spots. 400, imago; 401, worker caste.

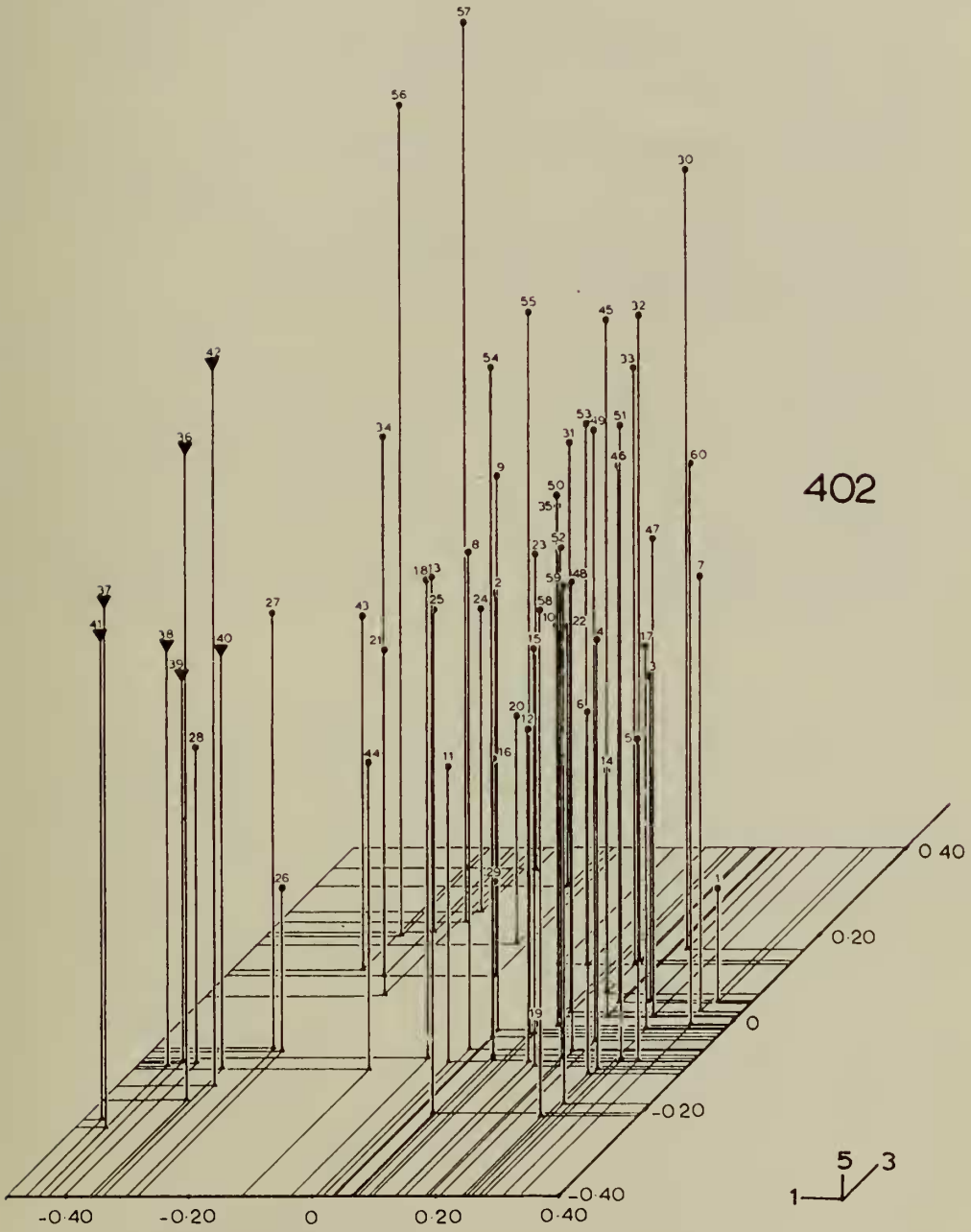


FIG. 402. Three-dimensional graph of principal co-ordinates analysis-plot of eigenvectors 1, 3 & 5 showing species of *Ateuchotermes* marked by large triangles.

- Compound eyes and ocelli smaller, W/E , 3.60-4.16, $O_w/O-E$, 0.71-1.80 (i.e. separated by more than half least diameter of ocellus) 3
- 2 Larger, W , 1.16-1.24. Postclypeus moderately inflated, Pcl/W , 0.27-0.28 *rastratus* (p. 171)
- Smaller, W , 0.98-1.04. Postclypeus scarcely inflated, Pcl/W , 0.23 *retifaciens* (p. 174)
- 3 Right mandible with anterior edge of first marginal tooth longer than that of second 4
- Right mandible with anterior edge of first marginal tooth equal to or shorter than that of second 6
- 4 Postclypeus strongly inflated, Pcl/W , 0.29. Fore tibia with third apical spur vestigial, nearly obsolete. Ocellus separated from compound eye by distinctly more than own least diameter, $O_w/O-E$, 0.71 *tranquillus* (p. 181)
- Postclypeus less inflated, Pcl/W , 0.23-0.26. Fore tibia with third apical spur smaller but not vestigial. Ocellus separated from compound eye by less than own least diameter or slightly more, $O_w/O-E$, 0.90-1.31 5
- 5 Fontanelle short oval, coloured as head capsule. Pilosity of head capsule forming a somewhat rough pelt with uneven emergent setae. (Distribution, E. Africa) *pectinatus* (p. 168)
- Fontanelle irregularly rounded triangular, paler than head. Pilosity of head capsule forming a short, fine, even pelt with emergent setae. (Distribution, W. Africa) *sentosus* (p. 176)
- 6 Smaller, W , 0.90-1.01. Ocelli slightly closer to compound eyes, $O_w/O-E$, 1.19-1.80 *ctenopher* (p. 163)
- Larger, W , 1.10-1.23. Ocelli further from compound eyes, $O_w/O-E$, 0.82-1.13 7
- 7 Apical teeth of mandibles longer, L_A/L_1 , 0.66, R_A/R_1 , 1.01. Mesonotum narrower at constriction, M/W , 0.26. *spinulatus* (p. 179)
- Apical teeth of mandibles shorter, L_A/L_1 , 0.50-0.60, R_A/R_1 , 0.70-0.84. Mesonotum wider at constriction, M/W , 0.28-0.34 *muricatus* (p. 165)

Workers

- 1 Enteric valve cushion in position 1 sclerotized only on distal half, only about one-quarter of total length of cushion protruding beyond tips of spines of other cushions; these spines stout and abruptly tapered at tips, not hooked (Pl. 4, fig. 5). Larger, W , 1.10. Enteric valve seating with distinct neck *tranquillus* (p. 181)
- Enteric valve cushion in position 1 sclerotized throughout its length, of which about half protrudes beyond tips of spines of other cushions; these spines more slender, more finely tapered at tips, sometimes hooked. Smaller, W , 0.75-0.99. Enteric valve seating sessile or nearly so 2
- 2 Left mandible with proximal end of subsidiary marginal tooth level with edge of molar prominence in surface view. Enteric valve cushions in positions 2, 3 and 4 with extremely long fine slender spines, each with a completely recurved hook at the tip, capable of engagement with other spines to form a criss-crossed network (Pl. 6, figs 6-8) *retifaciens* (p. 174)
- Left mandible with proximal end of subsidiary marginal tooth clear of molar prominence in surface view. Enteric valve cushions in positions 2, 3 and 4 with shorter, less fine spines, if hooked, tips not fully recurved, incapable of engagement with other spines as above 3
- 3 Smaller, W , 0.75-0.85. Apical teeth of mandibles shorter, L_A/L_1 , 0.45-0.58, R_A/R_1 , 0.59-0.74. Fore tibia slightly thicker, T_1/T_w , 4.72-5.10 4
- Larger, W , 0.91-0.99. Apical teeth of mandibles longer, L_A/L_1 , 0.64-0.74, R_A/R_1 , 0.86-1.01. Fore tibia thinner in most species, T_1/T_w , 5.05-5.90 (only one under 5.20) 5
- 4 Postclypeus more inflated, Pcl/W , 0.26-0.28. Enteric valve cushion 1 with dilated outer end inflated in the middle and armed with two rows of prominent spines,

- those of outer row numbering 30-40. Spines of other cushions slender, evenly tapered and nearly straight to their tips (Pl. 6, figs 1 & 2) *ctenopher* (p. 163)
- Postclypeus less inflated, Pcl/W, 0.22-0.24. Enteric valve cushion 1 with dilated outer end not inflated, flat in middle with a few scattered short spines and a single outer row of prominent spines numbering 14-18. Wall of enteric valve seating commonly with sclerotized cup which fits over spines of cushion 1. Spines of other cushions more tapered and slightly hooked at tips (Pl. 5, figs 7-9) *sentosus* (p. 176)
- 5 Right mandible with anterior edge of first marginal tooth equal to or longer than that of second. End of enteric valve cushion 1 armed with 15-23 spines (only one recorded over 20) 6
- Right mandible with anterior edge of first marginal tooth shorter than that of second. End of enteric valve cushion 1 armed with 23-40 spines (most specimens 25 or more) 7
- 6 Postclypeus more inflated, Pcl/W, 0.30. End of enteric valve cushion 1 more widely dilated (Pl. 5, figs 1-3) *rastratus* (p. 171)
- Postclypeus less inflated, Pcl/W, 0.27. End of enteric valve cushion 1 less widely dilated (Pl. 4, figs 6 & 7) *pectinatus* (p. 168)
- 7 Fore tibia slightly thicker, T_1/T_w , 5.05. Apical tooth of left mandible longer, $L_A/L_1.L_m$, 14.41. Mesenteric overlap with proctodeum at junction, length nearly three times width of mesenteron at insertion of malpighian tubules. Enteric valve cushions very narrow, positions 2-4 armed with long slender spines (Pl. 6, figs 3-5) *spinulatus* (p. 179)
- Fore tibia thinner, T_1/T_w , 5.35-5.90. Apical tooth of left mandible shorter, $L_A/L_1.L_m$, 10.28-13.06. Mesenteric overlap with proctodeum at junction about twice as long as width of mesenteron at insertion of malpighian tubules. Enteric valve cushions broader, positions 2-4 armed with stouter spines (Pl. 5, figs 4-6) *muricatus* (p. 165)

Ateuchotermes ctenopher sp. n.

(Text-figs 403, 404, 411, 412 & 419-444; Pl. 6, figs 1 & 2)

Imago. (Kings and Queens, colours may be faded.) Head capsule brown, sepia-brown above ocelli; fontanelle less than half size of ocellus, roughly circular, outline indistinct, flat or slightly depressed, pale yellow-brown; medial spot circular, flat or slightly raised, minute, coloured as head; postclypeus pale brown, labrum yellow; frontal marks very indistinct flat yellow-brown crescents; antennae pale yellow-brown. Pronotum, meso- and metanota pale brown, transverse dark sutures present; femora pale yellow-brown, tibiae paler, tarsi yellow-white. Abdominal tergites and dorsal stigmata pale yellow-brown, sternites and ventral stigmata very pale yellow-brown, sternites paler in middle, cerci yellow.

Posterior margin of head capsule not quite evenly rounded, slightly undulating, ocelli medium-sized, separated from compound eyes by from slightly over half to five-sixths own least diameter; postclypeus weakly to moderately inflated, Pcl/W, 0.23-0.26, posterior margin evenly rounded, median suture weakly developed. Apical teeth of mandibles short, L_A/L_1 , 0.54-0.64, R_A/R_1 , 0.69-0.84; subsidiary marginal tooth of left mandible with proximal end just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 7.40-9.10; point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edge of first marginal distinctly shorter than that of second. Meso- and metanota moderately wide at constriction, M/W, 0.28-0.31. Pilosity of head capsule yellow-brown, very even pelt with very sparse emergent setae, mostly paired bilaterally.

Measurements (three specimens from two localities) in millimetres.

	Range	Mean
Head width across eyes (W)	0.90-1.01	0.938
Ocellus ($O_w \times O_1$)	0.08-0.09 \times 0.10-0.13	0.084 \times 0.118
Ocellus to eye (O-E)	0.05-0.07	0.061
Postclypeus length (Pcl)	0.21-0.25	0.231
Antennal article III	0.03-0.05	0.035
Antennal article IV	0.04-0.05	0.048
Antennal article V	0.04-0.05	0.046
Left mandible, apical to first marginal (L_A)	0.07-0.09	0.082
Left mandible, first to third marginal (L_1)	0.13-0.16	0.143
Left mandible, third marginal to molar (L_m)	0.07-0.08	0.070
Right mandible, apical to first marginal (R_A)	0.07-0.09	0.082
Right mandible, first to second marginal (R_1)	0.10-0.13	0.111
Right mandible, second marginal to molar (R_m)	0.07-0.08	0.072
Mesonotum width (M)	0.25-0.31	0.279
Metanotum width (N)	0.29-0.34	0.306

Worker. Head capsule pale yellow, pilosity yellow, sparse. Postclypeus moderately inflated, Pcl/W, 0.26-0.28. Apical teeth of mandibles short, L_A/L_1 , 0.53-0.58, R_A/R_1 , 0.71-0.74; subsidiary marginal tooth of left mandible with proximal end just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 10.12-10.83; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal about half length of that of second, $R_A/R_1.R_m$, 12.13-13.80. Fore tibia scarcely swollen, T_1/T_w , 4.72-5.00, third apical spur nearly vestigial, about one-quarter length of other two. Mesenteric junction with proctodeum diagonal; enteric valve seating sessile on second pouch of proctodeum, very nearly dorsal in unopened abdomen; enteric valve cushion in position 1 sclerotized throughout its length, half of which protrudes beyond tips of spines of other positions, spines confined to dilated distal end, shaft smooth; spines on rim of dilated end 30-40 in number, middle portion of wider part inflated, with a second row of long spines, and scattered smaller spines behind them; cushions in other positions with 3-6 elongated curved spines, evenly tapered and almost straight at tips, few weakly hooked; membranous wall of valve beyond and between cushions without detectable spicules.

Measurements (two specimens from two localities) in millimetres.

Head width (W)	0.75-0.85
Fore tibia width (T_w)	0.11-0.12
Fore tibia length (T_1)	0.53-0.59
Postclypeus length (Pcl)	0.19-0.24
Left mandible, apical to first marginal (L_A)	0.07-0.08
Left mandible, first to third marginal (L_1)	0.13-0.14
Left mandible, third marginal to molar (L_m)	0.05-0.06
Right mandible, apical to first marginal (R_A)	0.07-0.08

Right mandible, first to second marginal (R ₁)	0.10-0.11
Right mandible, second marginal to molar (R _m)	0.05-0.06

This is the smallest species of *Ateuchotermes*, although its known size range overlaps with *A. retifaciens*. The latter is distinguishable in the imago by its large ocelli, very close to the compound eyes, and in the worker caste by its very long hooked enteric valve spines on cushions 2, 3, 4, together with the different position of the subsidiary marginal tooth of the left mandible. The vestigial third spur on the fore tibia, the large size and differently proportioned marginal teeth of the right mandible distinguish the imago of *A. tranquillus*, the worker of which is also larger with a less well-developed enteric valve, particularly cushion position 1. All the other imagos are larger, *A. muricatus* having the ocelli further from the eyes; *A. pectinatus*, *A. rastratus* and *A. sentosus* all have the anterior edge of the right first marginal tooth longer than that of the second, and *A. spinulatus* has longer apical teeth and narrower meso- and metanota. In the worker caste, none of the remaining species has the middle part of the dilated distal end of enteric valve cushion 1 inflated, and armed with a second row of spines; they are all flat or concave with scattered spines. The condition of this structure seen in *A. ctenopher* and *A. retifaciens* would seem to represent the end point in specialization.

Holotype queen, paratype workers from type-colony, GABON: 18 km from Makokou, 8.iii.1962 (*J. Deligne*) in Musée Royal de l'Afrique Centrale, Tervuren. (Paratype king and workers from type-colony in BMNH.)

Other paratype material. DEMOCRATIC REPUBLIC OF CONGO: Kwango River, Takundi, 14.v.1964 (*G. Mathot*), queen and workers, in Musée Royal de l'Afrique Centrale, Tervuren.

Both nest-series were collected from beneath nests of other species, the type-colony beneath *Crenetermes albotarsalis* (Sjöstedt) and the other paratypes from a *Cubitermes* mound. The species is only known from the main Congo rain forest block, the two records being from localities just over 450 miles apart.

Ateuchotermes muricatus sp. n.

(Text-figs 405, 406, 413, 414 & 425-431; Pl. 5, figs 4-6)

Imago. Head capsule sepia-brown, darker above ocelli and around compound eyes; fontanelle oval or circular, smaller than ocellus, margins indistinct, sometimes approaching triangular, flat or slightly depressed, brown or paler to near yellow-white; medial spot circular, flat, smaller than fontanelle, slightly paler than head; postclypeus sepia-brown, labrum brown; frontal marks distinct, flat, semicircular, coloured as head; antennae pale brown. Pronotum, meso- and metanota sepia-brown, transverse dark sutures weakly developed, particularly on mesonotum; femora and tibiae pale brown, tarsi yellow. Abdominal tergites and sternites brown, the latter paler in middle, dorsal and ventral stigmata both darker, sepia-brown; cerci pale yellow-brown.

Posterior margin of head capsule not evenly rounded, distinctly undulating; ocelli rather small, separated from compound eyes by slightly less to rather more than own least diameter;

postclypeus moderately to strongly inflated, Pcl/W, 0.28-0.34, posterior margin evenly rounded, median suture weakly developed or near absent. Apical teeth of mandibles short, L_A/L_1 , 0.50-0.60, R_A/R_1 , 0.70-0.84; subsidiary marginal tooth of left mandible well clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 5.33-7.72; points of apical and marginal teeth of right mandible almost in line, anterior edges of first and second marginals about equal in length. Meso- and metanota moderately wide at constriction, M/W, 0.28-0.34. Pilosity of head brown, pelt with uneven emergent setae.

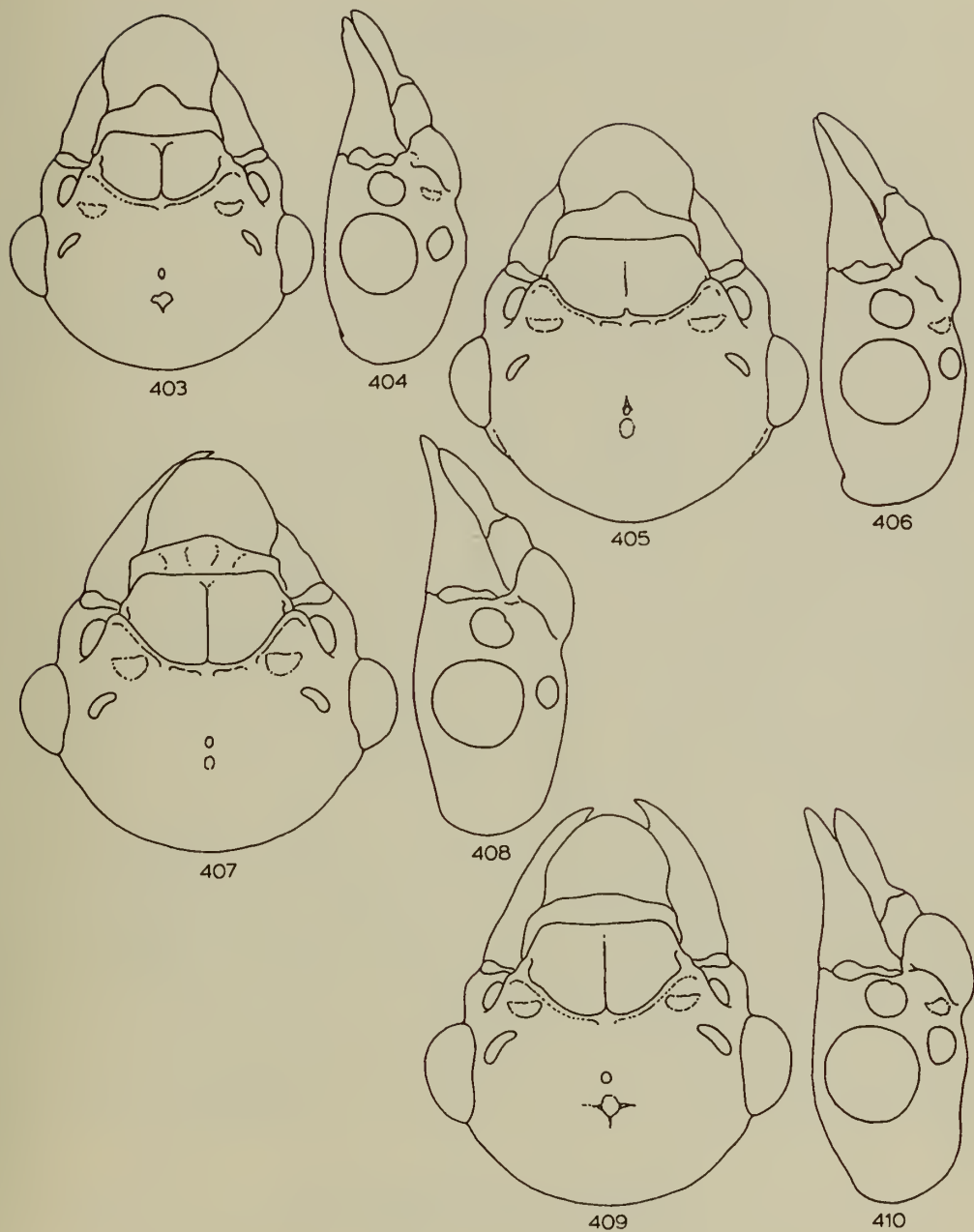
Measurements (six specimens from six localities) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	1.10-1.23	1.161 \pm 0.049
Ocellus ($O_w \times O_l$)	0.07-0.09 \times 0.09-0.13	0.077 \pm 0.006 \times 0.111 \pm 0.007
Ocellus to eye (O-E)	0.07-0.09	0.080 \pm 0.007
Postclypeus length (Pcl)	0.24-0.27	0.254 \pm 0.015
Antennal article III	0.03-0.05	0.043 \pm 0.006
Antennal article IV	0.05-0.06	0.058 \pm 0.005
Antennal article V	0.06-0.08	0.064 \pm 0.006
Left mandible, apical to first marginal (L_A)	0.08-0.11	0.094 \pm 0.007
Left mandible, first to third marginal (L_1)	0.16-0.19	0.174 \pm 0.010
Left mandible, third marginal to molar (L_m)	0.08-0.09	0.084 \pm 0.006
Right mandible, apical to first marginal (R_A)	0.09-0.10	0.095 \pm 0.005
Right mandible, first to second marginal (R_1)	0.12-0.14	0.128 \pm 0.007
Right mandible, second marginal to molar (R_m)	0.08-0.09	0.083 \pm 0.005
Mesonotum width (M)	0.31-0.40	0.360 \pm 0.029
Metanotum width (N)	0.34-0.40	0.375 \pm 0.017

Work. Head capsule pale yellow, pilosity yellow, sparse. Postclypeus weakly to moderately inflated, Pcl/W, 0.24-0.28. Apical teeth of mandibles fairly short, or a little longer, L_A/L_1 , 0.64-0.73, R_A/R_1 , 0.86-0.93; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio, $L_A/L_1.L_m$, 10.28-13.06; point of first marginal tooth of left mandible slightly behind line of apical to second marginal, anterior edges of first and second marginals approximately equal, or first slightly shorter, $R_A/R_1.R_m$, 13.68-17.10. Fore tibia slender, T_1/T_w , 5.35-5.90, third apical spur minute, vestigial, even absent in some specimens though seldom in all of one nest-series. Mesenteric junction with proctodeum slightly longer than diagonal; enteric valve seating with very short neck, nearly dorsal in unopened abdomen; enteric valve cushion in position 1 sclerotized throughout its length of which about half protrudes beyond tips of spines of other positions, dilated end ringed with 23-38 (average 29.4) elongated spines, shaft and concave surface of dilated end with scattered small spines, base of shaft wrinkled transversely; cushions in other positions with 1-10 (average 5.1) elongated curved spines, weakly hooked at tips, and smaller spines on remainder of length; membranous wall of valve between and beyond cushions without detectable spicules.

Measurements (five specimens from five localities) in millimetres.

	Range	Mean \pm S.D.
Head width (W)	0.91-0.98	0.948 \pm 0.029
Fore tibia width (T_w)	0.12-0.13	0.122 \pm 0.003
Fore tibia length (T_1)	0.66-0.74	0.695 \pm 0.039



FIGS 403-410. *Ateuchotermes*, imago head capsules, front and side views. 403, 404, *A. ctenoceph*; 405, 406, *A. muricatus*; 407, 408, *A. pectinatus*; 409, 410, *A. vastratus*.

Postclypeus length (Pcl)	0.22-0.26	0.244 ± 0.017
Left mandible, apical to first marginal (L _A)	0.09-0.10	0.095 ± 0.007
Left mandible, first to third marginal (L ₁) .	0.13-0.15	0.141 ± 0.008
Left mandible, third marginal to molar (L _m)	0.05-0.06	0.056 ± 0.006
Right mandible, apical to first marginal (R _A)	0.08-0.10	0.093 ± 0.008
Right mandible, first to second marginal (R ₁)	0.09-0.11	0.105 ± 0.009
Right mandible, second marginal to molar (R _m)	0.05-0.06	0.058 ± 0.005

A. muricatus has already been compared with *A. ctenopher* under the latter heading. *A. retifaciens* is distinguished by the same characters that separate it from *A. ctenopher*, as also is *A. tranquillus*. The differing mandible proportions again characterize the remaining species in the imago. In the worker caste *A. sentosus* is smaller, and the wall of the enteric valve seating bears a sclerotized cup that receives the dilated end of cushion 1. *A. rastratus* and *A. pectinatus* have the outer edge of the right first marginal tooth longer than the second, and *A. spinulatus* has longer apical teeth, and slender spines on the enteric valve cushions in positions 2-4. The enteric valve of *A. muricatus* seems intermediate in development between the forms seen in *A. rastratus* and *A. pectinatus*, and the 'slender' form of *A. spinulatus*. It shows a fair amount of variation between specimens from Malawi and South Africa, and there is a possibility that two species have been combined here. However, separation would not seem to be justified at present without more material and information since there are intermediate specimens.

Holotype ♀ winged imago, and three paratype workers from type-colony, REPUBLIC OF SOUTH AFRICA: Transvaal, Sibasa, 9.vii.1960 (*J. L. Sheasby*) in National Collection of Isoptera, Coll. No. TM 7413, Pretoria.

Other paratype material. REPUBLIC OF SOUTH AFRICA: Transvaal, Carolina, 22.xii.1955 (*W. G. H. Coaton*); Ermelo, 6.vi.1956 (*J. H. Grobler*); Carolina, 26.x.1960 (*J. L. Sheasby*), alates and workers. SWAZILAND: Mbabane, 23.x.1960 (*W. G. H. Coaton*) alates and workers, all above in N.C.I., Pretoria. MALAWI: Vipya Plateau, 6 m. N. of Mount Chioli (two vials) 20.ix.1953, king and workers, 7 m. from Kota-Kota on Kasungu Road, 17.ix, 33 m. from Kasungu on Lilongwe Road, 18.ix, Nyika Plateau (two vials) 29.ix, and Songwe, 1.x.1953, all workers only (*W. A. Sands & W. Wilkinson*), all in BMNH.

Most of the records are from the low mounds of *Cubitermes* spp., only one series being found under dead wood in an area of tall dense woodland approaching rain forest conditions.

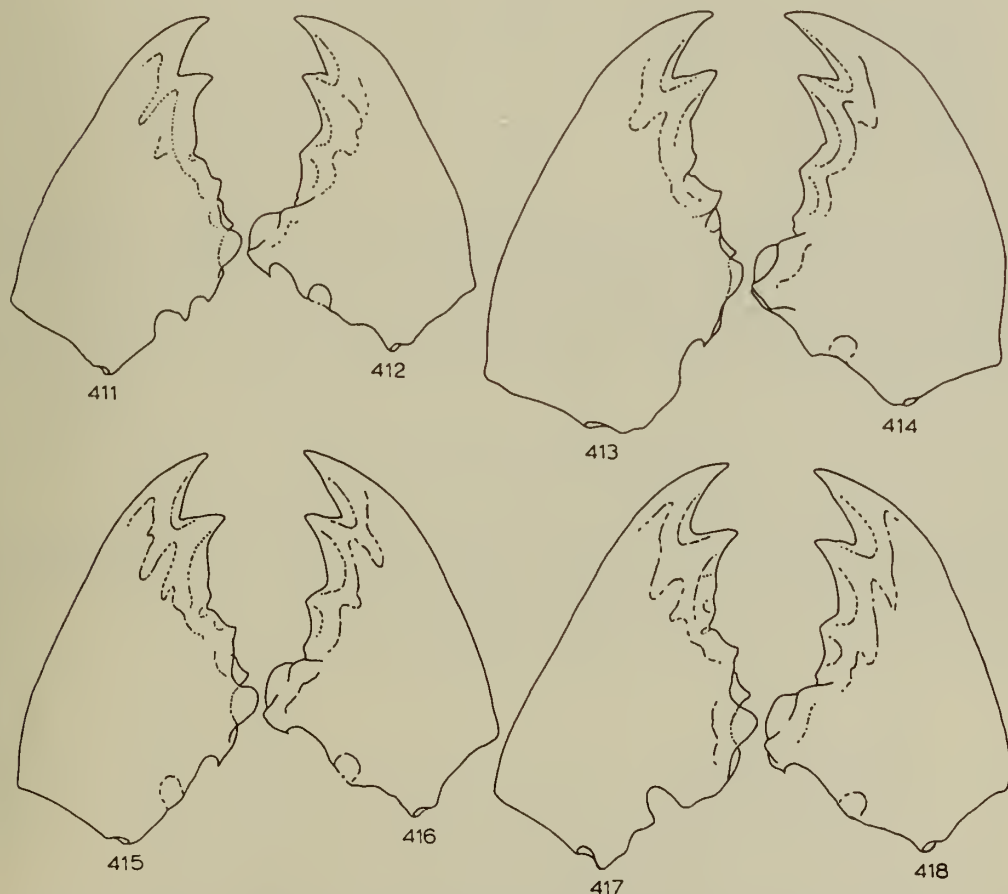
Ateuchotermes pectinatus sp. n.

(Text-figs 407, 408, 415, 416 & 432-438; Pl. 4, figs 6 & 7)

Imago. Head capsule dark chestnut-brown, not darker above ocelli; fontanelle much smaller than ocellus, circular to short oval indistinct outline, flat or slightly depressed, coloured as head; medial spot circular or broad oval, flat or slightly raised, equal in size to fontanelle or slightly

larger, coloured as head; postclypeus chestnut-brown, labrum yellow-brown; frontal marks distinct, semicircular, flat or slightly depressed, brown; antennae brown. Pronotum, meso- and metanota chestnut-brown, transverse dark sutures weak on mesonotum, present on metanotum; femora and tibiae brown, tarsi yellow. Abdominal tergites brown, dorsal stigmata dark sepia-brown, sternites pale brown, yellow-brown in middle, ventral stigmata sepia-brown; cerci pale yellow-brown.

Posterior margin of head capsule not quite evenly rounded, slightly undulating; ocelli proportionately rather small, separated from compound eyes by about three-quarters, up to slightly more than own least diameter; postclypeus weakly to moderately inflated, PcI/W , 0.23-0.26, posterior margin bowed, not evenly rounded, median suture distinct. Apical teeth of mandibles short, L_A/L_1 , 0.54-0.60, R_A/R_1 , 0.73-0.89; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio, $L_A/L_1.L_m$, 5.90-7.84; points of apical and marginal teeth of right mandible in line, anterior edge of first marginal longer than that of second. Meso- and metanota fairly wide at constriction, M/W , 0.29-0.33. Pilosity of head capsule yellow-brown, pelt somewhat rough, slightly uneven.



FIGS 411-418. *Ateuchotermes*, imago mandibles. 411, 412, *A. clenopher*; 413, 414, *A. muricatus*; 415, 416, *A. pectinatus*; 417, 418, *A. vastratus*.

Measurements (seven specimens from four localities) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	1.04-1.30	1.177 \pm 0.089
Ocellus ($O_w \times O_l$)	0.08-0.13 \times 0.11-0.15	0.092 \pm 0.020 \times 0.131 \pm 0.016
Ocellus to eye (O-E)	0.08-0.10	0.087 \pm 0.007
Postclypeus length (Pcl)	0.24-0.31	0.285 \pm 0.022
Antennal article III	0.03-0.08	0.045 \pm 0.017
Antennal article IV	0.06-0.09	0.066 \pm 0.012
Antennal article V	0.05-0.08	0.064 \pm 0.011
Left mandible, apical to first marginal (L_A)	0.09-0.10	0.096 \pm 0.004
Left mandible, first to third marginal (L_1)	0.16-0.19	0.173 \pm 0.010
Left mandible, third marginal to molar (L_m)	0.08-0.09	0.085 \pm 0.006
Right mandible, apical to first marginal (R_A)	0.09-0.11	0.100 \pm 0.005
Right mandible, first to second marginal (R_1)	0.11-0.14	0.124 \pm 0.011
Right mandible, second marginal to molar (R_m)	0.08-0.10	0.087 \pm 0.007
Mesonotum width (M)	0.33-0.41	0.366 \pm 0.038
Metanotum width (N)	0.33-0.43	0.380 \pm 0.036

Worker. Head capsule and pilosity pale yellow, setae sparsely scattered. Postclypeus moderately inflated, Pcl/W, 0.27. Apical teeth of mandibles fairly long, L_A/L_1 , 0.70-0.71, R_A/R_1 , 1.00-1.01; subsidiary marginal tooth of left mandible separated from molar prominence by deep notch in surface view, complex ratio $L_A/L_1.L_m$, 8.90-11.09; point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edges of first and second marginals equal, $R_A/R_1.R_m$, 14.99-15.05. Fore tibia slender, T_1/T_w , 5.29-5.64, third apical spur vestigial, even absent in some specimens, rarely in all of any nest series. Mesenteric junction with proctodeum diagonal; enteric valve seating connected to second pouch of proctodeum by very short neck, dorsolateral in unopened abdomen; enteric valve cushion in position 1 sclerotized throughout its length, half of which protrudes beyond tips of spines of other positions, dilated end fringed with 15-18 (average 16.3) elongated spines, shaft and concave surface of dilated end with scattered small spines, base of shaft weakly wrinkled transversely; cushions in other positions with 3-5 (average 3.5) elongated curved spines, sharply tapered and weakly hooked at tips, and smaller spines on remainder of length. Membranous wall of valve beyond and between cushions with definite spicules fringing small lobes.

Measurements (three specimens from three localities) in millimetres.

	Range	Mean
Head width (W)	0.94-0.99	0.967
Fore tibia width (T_w)	—	0.127
Fore tibia length (T_1)	0.69-0.71	0.700
Postclypeus length (Pcl)	0.25-0.27	0.260
Left mandible, apical to first marginal (L_A)	0.10-0.11	0.105
Left mandible, first to third marginal (L_1)	0.14-0.15	0.148
Left mandible, third marginal to molar (L_m)	0.06-0.08	0.071
Right mandible, apical to first marginal (R_A)	0.10-0.11	0.107
Right mandible, first to second marginal (R_1)	0.10-0.11	0.106
Right mandible, second marginal to molar (R_m)	0.07-0.08	0.070

Comparisons have already been made between *A. pectinatus*, *A. ctenopher* and *A. muricatus*. In the imago caste, *A. rastratus* and *A. retifaciens* have larger eyes and ocelli closer together, than in *A. pectinatus*. The reverse is true of *A. tranquillus*, which also has a more inflated postclypeus and vestigial third apical spur on the fore tibia. *A. sentosus* has more even head pilosity, and a differently shaped fontanelle. *A. spinulatus* has longer apical mandibular teeth, and narrower meso- and metanota. In the worker caste, *A. rastratus* is difficult to distinguish from *A. pectinatus*, having a slightly more inflated postclypeus and possibly a somewhat wider dilation at the end of enteric valve cushion 1, though this may not be constant. The sclerotized cup and fenestrated base of enteric valve cushion 1 distinguish *A. sentosus*, as well as its smaller size. The longer apical teeth of the mandibles and slender spines on enteric valve cushions 2, 3 and 4 distinguish *A. spinulatus*, also the more numerous spines fringing cushion 1. In *A. tranquillus* the enteric valve armature is less well developed, position 1 being only partly sclerotized and shorter. In *A. retifaciens* it reaches the other extreme with elongated hooked spines in positions 2, 3 and 4.

Holotype ♀ imago, paratype ♂ and ♀ imagos and workers from type-colony, KENYA: Kaptagat Forest, alt. 8,000 ft, 2.iv.1952 (*W. V. Harris* Coll. No. 826) in British Museum (Natural History).

Other paratype material. KENYA: Kaptagat, 3.iv.1952 (*W. A. Sands*); Londiani, alt. 8,100 ft, 18.ii.1954 (*R. M. C. Williams*). UGANDA: Ruwenzori, Fort Portal, 1952 (*H. A. Osmaston*), alates and workers, all above in BMNH. DEMOCRATIC REPUBLIC OF CONGO: Kivu, Lwiro (two vials), 24. 5.x, Irangi, 1°53'S., 28°28'E., 10.xi.1963 (*E. Ernst*), workers only, in BMNH and Swiss Tropical Institute, Basle.

All the biological information on this species points to its being an inhabitant of the mounds of other species, either *Cubitermes* or *Odontotermes*, at considerable altitudes.

Ateuchotermes rastratus sp. n.

(Text-figs 409, 410, 417, 418 & 439-444; Pl. 5, figs 1-3)

Imago. Head capsule chestnut-brown, darker above ocelli; fontanelle roughly circular, slightly depressed, much smaller than ocellus, pale yellow-brown; medial spot circular, flat, smaller than fontanelle, coloured as head; postclypeus paler than head, ferruginous chestnut-brown, labrum yellow-brown; frontal marks, very indistinct flat crescents, coloured as postclypeus; antennae yellow. Pronotum, meso- and metanota brown, transverse sutures virtually absent; femora pale yellow-brown, tibiae and tarsi yellow. Abdominal tergites brown, dorsal stigmata yellow-brown, sternites yellow-brown with middle and ventral stigmata paler; cerci yellow.

Posterior margin of head capsule slightly undulating, not quite evenly rounded; ocelli proportionately fairly large, separated from large compound eyes by less than half own least diameter; postclypeus moderately inflated, Pcl/W, 0.27-0.28, posterior margin bowed, not evenly rounded, median suture distinct. Apical teeth of mandibles short, L_A/L_1 , 0.56-0.62, R_A/R_1 , 0.80-0.92; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio, $L_A/L_1.L_m$, 6.88-8.20; points of apical and marginal teeth of right mandible in line, anterior edge of first marginal longer than that of second. Meso- and metanota fairly wide at constriction, M/W, 0.30. Pilosity of head capsule yellow-brown, rather long, forming slightly uneven pelt.

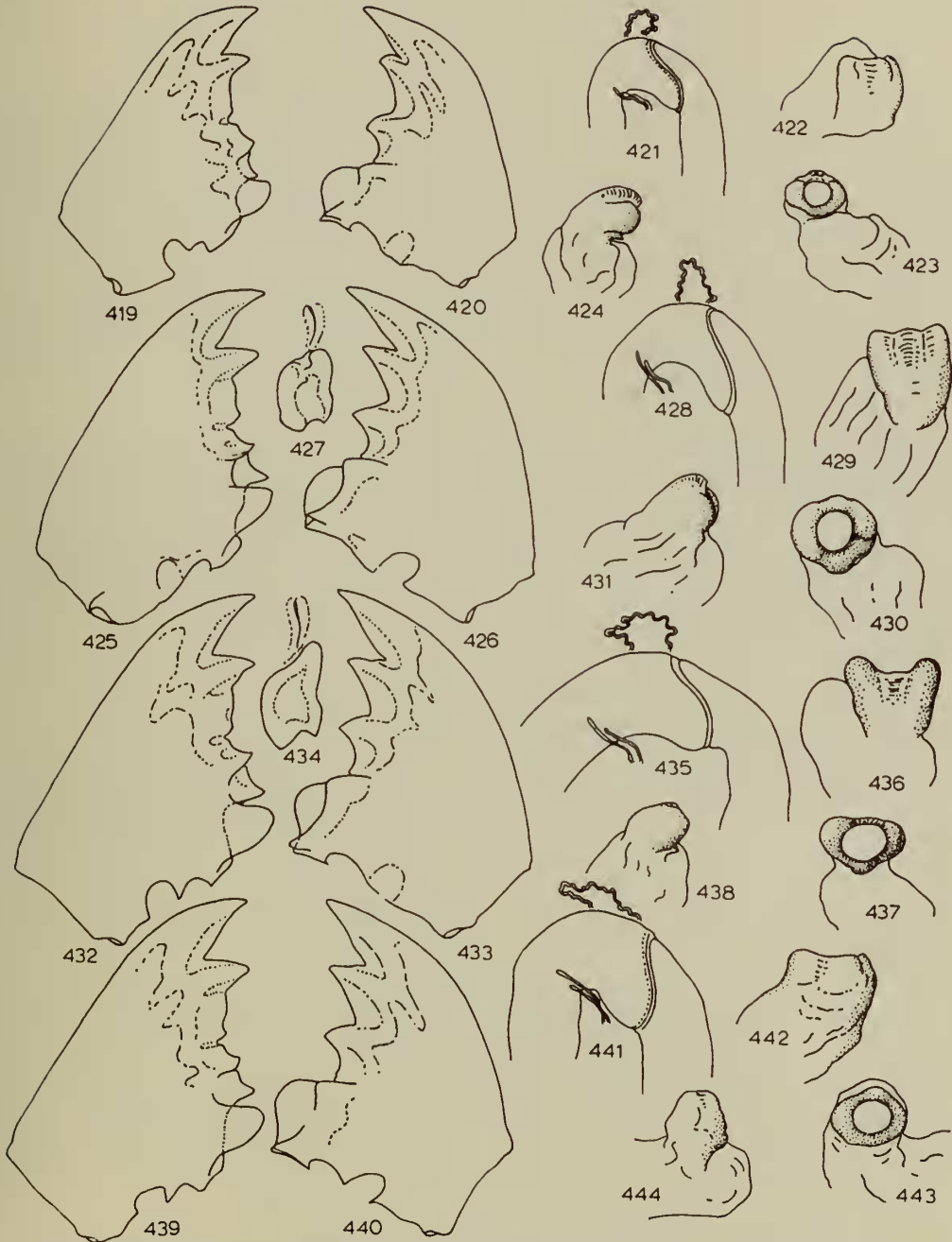
Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	1.16-1.24
Ocellus ($O_w \times O_l$)	0.11-0.12 \times 0.15
Ocellus to eye (O-E)	0.03-0.05
Postclypeus length (Pcl)	0.31-0.34
Antennal article III	0.04-0.05
Antennal article IV	0.05-0.06
Antennal article V	0.05-0.06
Left mandible, apical to first marginal (L_A)	0.10
Left mandible, first to third marginal (L_1)	0.16-0.18
Left mandible, third marginal to molar (L_m)	0.08-0.09
Right mandible, apical to first marginal (R_A)	0.10
Right mandible, first to second marginal (R_1)	0.11-0.13
Right mandible, second marginal to molar (R_m)	0.08-0.09
Mesonotum width (M)	0.35-0.37
Metanotum width (N)	0.38

Worker. Head capsule pale yellow, pilosity yellow, sparsely scattered. Postclypeus moderately inflated, Pcl/W, 0.30. Apical teeth of mandibles fairly long, L_A/L_1 , 0.72-0.74, R_A/R_1 , 0.96; subsidiary marginal tooth of left mandible separated from molar prominence by deep notch in surface view, complex ratio, $L_A/L_1.L_m$, 11.19-11.50; points of apical and marginal teeth of right mandible very nearly in line, anterior edge of first marginal slightly longer than that of second, equal if worn, $R_A/R_1.R_m$, 13.52-15.27. Fore tibia slender, T_1/T_w , 5.20-5.64, third apical spur smaller than other two, vestigial or up to nearly half their length. Mesenteric junction with proctodeum diagonal; enteric valve seating practically sessile on second pouch of proctodeum, dorsolateral in unopened abdomen; enteric valve cushion in position 1 sclerotized throughout its length, half of which protrudes beyond tips of spines of other positions, dilated and fringed with 15-23 (average 18.5) spines, shaft and concave surface of dilated end with scattered small spines, base of shaft distinctly transversely wrinkled; cushions in other positions with 2-7 (average 4.3) elongated curved spines, sharply tapered and distinctly hooked at tips, and smaller spines on remainder of length. Membranous wall of valve beyond and between cushions with definite spicules fringing small lobes.

Measurements (two specimens from one locality) in millimetres.

Head width (W)	0.91-0.98
Fore tibia width (T_w)	0.13
Fore tibia length (T_1)	0.65-0.72
Postclypeus length (Pcl)	0.27-0.29
Left mandible, apical to first marginal (L_A)	0.11
Left mandible, first to third marginal (L_1)	0.15
Left mandible, third marginal to molar (L_m)	0.06-0.07
Right mandible, apical to first marginal (R_A)	0.11



FIGS 419-444. *Ateuchotermes*, worker mandibles, mesenteric-proctodeal junctions showing attachments of malpighian tubules and position of malpighian knot, and views of enteric valve seatings. 419-424, *A. clenopher*; 425-431, *A. muricatus*; 432-438, *A. pectinatus*; 439-444, *A. rastratus*. (427 & 434 show right molar plate in surface view.)

Right mandible, first to second marginal (R_1)	0.11
Right mandible, second marginal to molar (R_m)	0.06-0.07

A. rastratus is compared with *A. ctenopher*, *A. muricatus* and *A. pectinatus* under those species. In the imago caste, it differs from all the remaining species other than *A. retifaciens* in having rather large eyes and ocelli, close together. The latter species is smaller, with a feebly inflated postclypeus, and the ocelli even closer to the eyes. In the worker, *A. retifaciens* has two rows of spines on the dilated end of enteric valve cushion 1, and long, slender, hooked spines on positions 2, 3 and 4. *A. sentosus* is again recognizable by the fenestrated base and sclerotized cup of position 1, *A. spinulatus* by the more numerous spines on position 1 and the slender spines in the other positions, and *A. tranquillus* by the incomplete sclerotization of the shorter cushion position 1.

Holotype ♀ imago, paratype ♂ and ♀ imagos and workers from type-colony, KENYA: Nyambeni Hills, 22 m. from Meru, alt. 4,000 ft, 21.ii.1953 (*W. A. Sands*, Coll. No. S409) in British Museum (Natural History).

Other paratype material. TANZANIA: Amani, Kizugu, 3.xi.1950, queen and workers, Amani, Monga Road, 2.iii.1951 (*P. B. Kemp*), workers only, in BMNH.

This species was found in low amorphous mounds apparently of its own construction, and under dead wood.

Ateuchotermes retifaciens sp. n.

(Text-figs 445-447, 454, 455 & 462-467; Pl. 6, figs 6-8)

Imago. Head capsule brown, not darker above ocelli; fontanelle irregularly oval, almost vestigial, much smaller than ocellus, flat or slightly depressed, pale or yellow-brown; medial spot oval, flat, nearly equal in size to fontanelle, slightly paler than head; postclypeus pale yellow-brown, labrum pale yellow; frontal marks pale yellow-brown, flat crescents; antennae yellow. Pronotum pale brown, meso- and metanota pale yellow-brown, transverse sutures virtually absent; femora pale yellow, tibiae and tarsi yellow-white. Abdominal tergites and dorsal stigmata pale brown, sternites and ventral stigmata very pale brown, middles of sternites and cerci pale yellow.

Posterior margin of head capsule evenly rounded; ocelli and compound eyes both large, and almost touching, maximum separation less than a quarter own least diameter; postclypeus weakly inflated, Pcl/W, 0.23, posterior margin evenly rounded, median suture present in ♀, weak in ♂. Apical teeth of mandibles short, L_A/L_1 , 0.53-0.55, R_A/R_1 , 0.75-0.77; subsidiary marginal tooth of left mandible distinctly clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 6.10-6.87; points of apical and marginal teeth of right mandible in line, anterior edge of first marginal longer than that of second. Meso- and metanota moderately wide at constriction, M/W, 0.29-0.33. Pilosity of head capsule very pale brown, an even pelt with scattered emergent setae.

Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	0.98-1.04
Ocellus ($O_w \times O_l$)	0.11-0.12 \times 0.13-0.14
Ocellus to eye (O-E)	0.02-0.03
Postclypeus length (Pcl)	0.23-0.24

Antennal article III	0.04-0.05
Antennal article IV	0.06
Antennal article V	0.06
Left mandible, apical to first marginal (L_A)	0.08
Left mandible, first to third marginal (L_1)	0.14
Left mandible, third marginal to molar (L_m)	0.08-0.09
Right mandible, apical to first marginal (R_A)	0.08-0.09
Right mandible, first to second marginal (R_1)	0.11
Right mandible, second marginal to molar (R_m)	0.08
Mesonotum width (M)	0.29-0.34
Metanotum width (N)	0.30-0.36

Worker. Head capsule pale yellow, pilosity yellow, sparse. Postclypeus moderately inflated, Pcl/W, 0.27. Apical teeth of mandibles short, L_A/L_1 , 0.53, R_A/R_1 , 0.68; subsidiary marginal tooth of left mandible with proximal end just level with edge of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 8.40; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal shorter than that of second, $R_A/R_1.R_m$, 10.40. Fore tibia scarcely swollen, T_1/T_w , 5.10, third apical spur about one-third length of other two. Mesenteric junction with proctodeum diagonal; enteric valve seating with short neck, dorsolateral in unopened abdomen; enteric valve cushion in position 1 sclerotized throughout its length, half of which protrudes beyond tips of spines of other positions, spines confined to dilated distal end, shaft smooth; spines on rim of dilated end 30-40, in number, middle portion of wider part inflated with a second row of long spines, and scattered long and smaller spines behind them; cushions in other positions with 7-10 extremely elongated straight slender spines, each tipped with a completely recurved hook, capable of engaging upon spines of other positions to form a criss-cross network; membranous wall of valve between and beyond cushions without detectable spicules.

Measurements (one specimen) in millimetres.

Head width (W)	0.96
Fore tibia width (T_w)	0.14
Fore tibia length (T_1)	0.70
Postclypeus length (Pcl)	0.26
Left mandible, apical to first marginal (L_A)	0.08
Left mandible, first to third marginal (L_1) .	0.15
Left mandible, third marginal to molar (L_m)	0.06
Right mandible, apical to first marginal (R_A)	0.09
Right mandible, first to second marginal (R_1)	0.13
Right mandible, second marginal to molar (R_m)	0.06

Comparisons have already been made between *A. retifaciens* and the preceding species, *A. ctenopher*, *A. muricatus*, *A. pectinatus* and *A. rastratus*. It is a distinctive species in the imago in having such large eyes and ocelli; and in this it differs from

the remaining three species, *A. sentosus*, *A. spinulatus* and *A. tranquillus*. The enteric valve armature of the worker caste, with its extremely long hooked spines, also serves to distinguish it clearly from these species. Even *A. spinulatus*, which has thin elongated spines, cannot be confused in this respect, especially since it also has longer apical mandibular teeth, and the subsidiary marginal tooth of the left mandible clear of the molar prominence.

Holotype queen, and paratype workers from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Kivu, Irangi, 1°53'S., 28°28'E., 9.xi.1963 (*E. Ernst*), in British Museum (Natural History); paratype king and workers from type-colony, in Swiss Tropical Institute, Basle.

The smaller nest-chambers of this species were found beneath a typical mound of *Thoracotermes macrothorax* (Sjöstedt) against a tree in rain forest.

Ateuchotermes sentosus sp. n.

(Text-figs 448, 449, 456, 457 & 468-473; Pl. 5, figs 7-9)

Imago. Head capsule sepia-brown, not darker above ocelli; fontanelle about half size of ocellus, irregular short oval, flat, brown; medial spot short oval, flat, smaller than fontanelle, coloured as head; postclypeus brown, labrum yellow-brown; frontal marks smooth flat crescents, coloured as postclypeus; antennae pale yellow-brown. Pronotum brown, meso- and metanota yellow-brown, transverse dark sutures weakly developed; femora yellow, tibiae paler, tarsi yellow-white. Abdominal tergites and dorsal stigmata yellow-brown, sternites paler, ventral stigmata paler than sternites; cerci yellow.

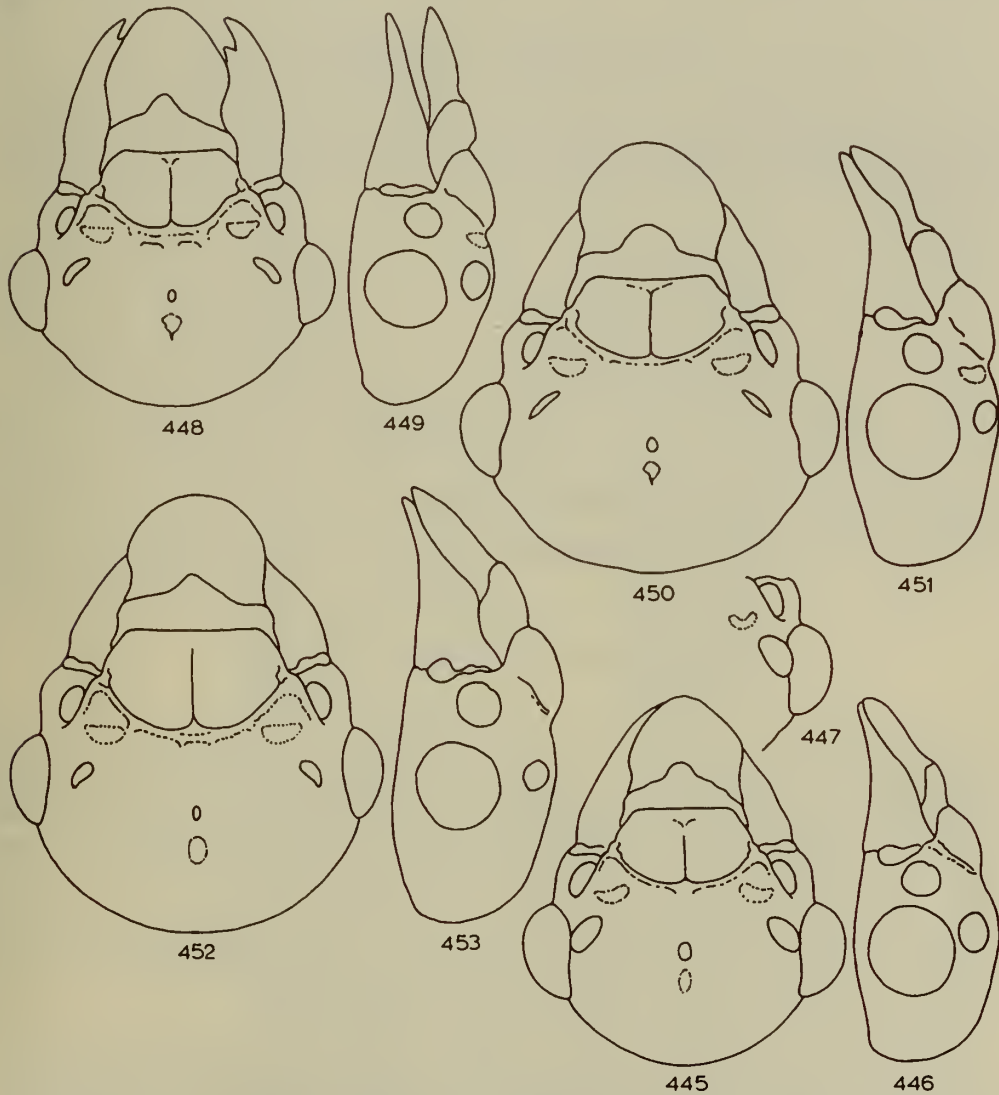
Posterior margin of head capsule slightly undulating, not evenly rounded; ocelli fairly large, separated from compound eyes by about three-quarters own least diameter; postclypeus weakly inflated, Pcl/W, 0.25, posterior margin somewhat indistinct, bowed, not evenly rounded, median suture distinct. Apical teeth of mandibles short, L_A/L_1 , 0.54, R_A/R_1 , 0.83; subsidiary marginal tooth of left mandible with proximal end just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 6.45; points of apical and marginal teeth of right mandible in line, anterior edge of first marginal longer than that of second. Meso- and metanota fairly wide at constriction. M/W, 0.33. Pilosity of head capsule a fine close even pelt with emergent setae.

Measurements (one specimen) in millimetres.

Head width across eyes (W)	1.04
Ocellus ($O_w \times O_1$)	0.09 × 0.13
Ocellus to eye (O-E)	0.07
Postclypeus length (Pcl)	0.26
Antennal article III	0.04
Antennal article IV	0.06
Antennal article V	0.06
Left mandible, apical to first marginal (L_A)	0.09
Left mandible, first to third marginal (L_1)	0.17
Left mandible, third marginal to molar (L_m)	0.08
Right mandible, apical to first marginal (R_A)	0.10

Right mandible, first to second marginal (R_1)	0·12
Right mandible, second marginal to molar (R_m)	0·09
Mesonotum width (M)	0·34
Metanotum width (N)	0·38

Worker. Head capsule and pilosity pale yellow, setae sparse. Postclypeus weakly inflated, Pcl/W , 0·22–0·24. Apical teeth of mandibles short, L_A/L_1 , 0·45–0·48. R_A/R_1 , 0·59–0·65;



FIGS 445-453. *Ateuchotermes*, imago head capsules, front and side views. 445-447, *A. retifaciens*, 447 shows compound eye and ocellus of ♂; 448, 449, *A. sentosus* ♂; 450, 451, *A. spinulatus*; 452, 453, *A. tranquillus*.

subsidiary marginal tooth of left mandible with proximal end just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 8.32-8.45; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal about half length of second, $R_A/R_1.R_m$, 10.91-11.52. Fore tibia scarcely swollen, T_1/T_w , 4.80-5.10, third apical spur vestigial, up to one-quarter length of other two. Mesenteric junction with proctodeum slightly longer than diagonal; enteric valve seating virtually sessile on second pouch of proctodeum, dorsolateral to nearly dorsal in unopened abdomen; enteric valve cushion in position 1 sclerotized throughout its length, half of which protrudes beyond tips of spines of other positions, spines confined to proximal and distal ends, shaft smooth; spines on rim of dilated distal end 14-20 in number, middle part of dilation rounded with scattered fairly long spines, base of shaft fenestrated with a minute spine in each 'hole'; wall of enteric valve seating adjacent to dilated end of position 1, indented and sclerotized in the form of a rounded cup, into which the spines of position 1 fit neatly; this cup sclerotization purplish-brown when fully developed, not yellow-brown as are the cushions of the valve; cushions in other positions with 3-6 elongated curved spines, weakly hooked at tips, and smaller spines on rest of length; membranous wall of valve between and beyond cushions with faint trace of spicules.

Measurements (two specimens) in millimetres.

Head width (W)	0.84-0.85
Fore tibia width (T_w)	0.12
Fore tibia length (T_1)	0.59-0.61
Postclypeus length (Pcl)	0.19-0.20
Left mandible, apical to first marginal (L_A)	0.06
Left mandible, first to third marginal (L_1)	0.13
Left mandible, third marginal to molar (L_m)	0.05-0.06
Right mandible, apical to first marginal (R_A)	0.06-0.07
Right mandible, first to second marginal (R_1)	0.10-0.11
Right mandible, second marginal to molar (R_m)	0.05-0.06

A. sentosus has already been compared with *A. ctenopher*, *A. muricatus*, *A. pectinatus*, *A. rastratus* and *A. retifaciens*, in the descriptions to those species. *A. tranquillus* differs from *A. sentosus* in the imago in having a vestigial third apical spur of the fore tibia, a more inflated postclypeus, and proportionately smaller eyes and ocelli, separated by more than the least diameter of the latter. The worker castes are easily recognized by their very distinctive enteric valve armature. *A. spinulatus* has, again, a distinctive worker caste, with the additional character of longer apical mandibular teeth in both worker and imago, the latter caste also having a proportionately shorter right second marginal tooth.

It should be noted here that the workers and imago of *A. sentosus* are associated on a basis of probability rather than certainty, since they were not found together. To do this is always risky, but since the workers have been found both in nearby and in more distant rain forest localities, and no other species is known from the vicinity, the probability that they are correctly associated is high.

Holotype, ♂ dealate, unique, NIGERIA: Port Harcourt, 19.X.1957 (*W. Wilkinson*, No. 841/A) in British Museum (Natural History).

Paratypes. NIGERIA: Benin Province, Obanokoro, Sobo Plain (two vials), 10.I.1957 (*W. Wilkinson*), workers only, in BMNH. GUINEA: Mount Nimba (*M. Lamotte*) in AMNH.

The only biological information on this species is that it was found in and under damp rotting logs in forest.

Ateuchotermes spinulatus sp. n.

(Text-figs 450, 451, 458, 459 & 474-479; Pl. 6, figs 3-5)

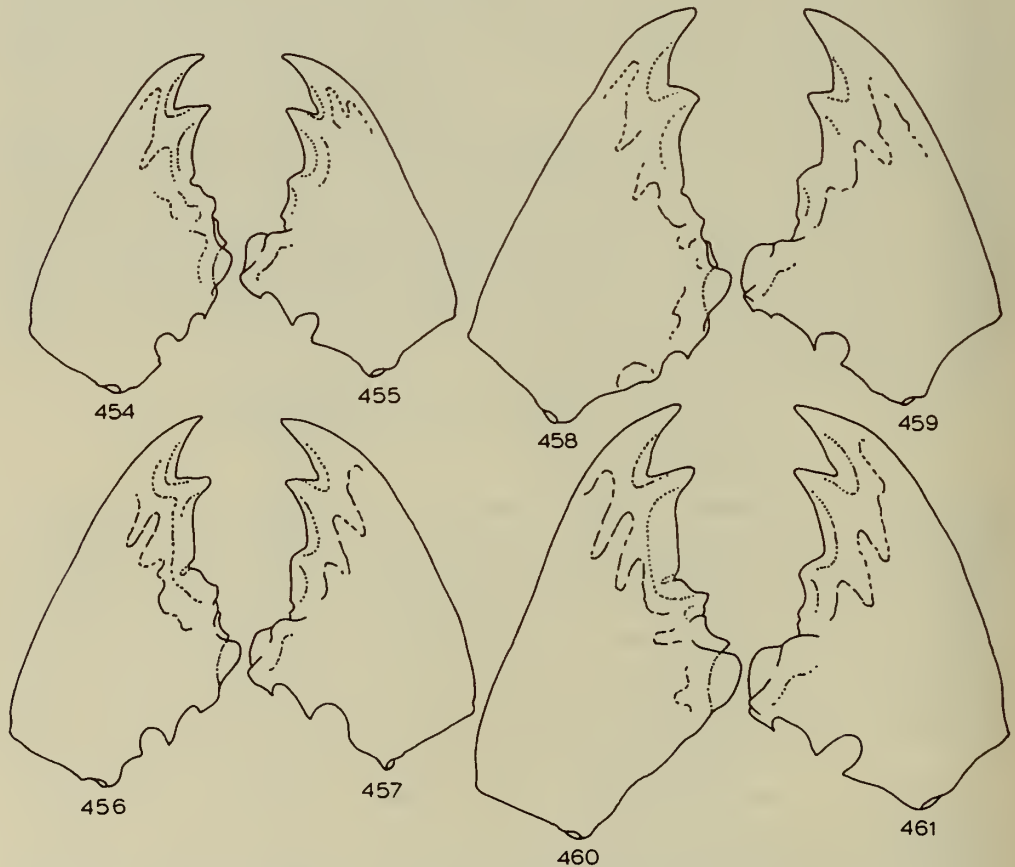
Imago. (Queen, colours may be faded.) Head capsule chestnut-brown, darker above ocelli; fontanelle roughly circular, with tendency towards triangular outline, slightly depressed, less than half size of ocellus, yellow-brown; medial spot circular, flat, slightly smaller than fontanelle, coloured as head; postclypeus chestnut-brown, labrum yellow-brown; frontal marks distinct, smooth, semicircular, slightly depressed, coloured as head; antennae brown. Pronotum, meso- and metanota, chestnut-brown, transverse dark sutures present, weak on mesonotum; femora brown, tibiae yellow-brown, tarsi yellow. Abdominal tergites brown, dorsal stigmata distinct, dark sepia-brown, sternites brown, pale brown in middle, ventral stigmata sepia-brown; cerci yellow-brown.

Posterior margin of head capsule not quite evenly rounded, slightly undulating; ocelli medium sized, separated from compound eyes by distinctly more than own least diameter; postclypeus weakly inflated, Pcl/W, 0.23, posterior margin evenly rounded, median suture weak. Apical teeth of mandibles fairly short, L_A/L_1 , 0.66, R_A/R_1 , 1.01; subsidiary marginal tooth of left mandible with proximal end just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 7.40-9.10; point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edge of first marginal equal to or slightly shorter than that of second. Meso- and metanota rather narrow at constriction, M/W, 0.26. Pilosity of head capsule a somewhat irregular pelt with emergent setae.

Measurements (one specimen) in millimetres.

Head width across eyes (W)	1.21
Ocellus ($O_w \times O_l$)	0.09 × 0.14
Ocellus to eye (O-E)	0.11
Postclypeus length (Pcl)	0.28
Antennal article III	0.05
Antennal article IV	0.06
Antennal article V	0.06
Left mandible, apical to first marginal (L_A)	0.13
Left mandible, first to third marginal (L_1)	0.19
Left mandible, third marginal to molar (L_m)	0.08
Right mandible, apical to first marginal (R_A)	0.13
Right mandible, first to second marginal (R_1)	0.13
Right mandible, second marginal to molar (R_m)	0.09
Mesonotum width (M)	0.32
Metanotum width (N)	0.36

Worker. Head capsule pale yellow, pilosity sparse, yellow. Postclypeus moderately inflated, Pcl/W , 0.27. Apical teeth of mandibles fairly long, L_A/L_1 , 0.74, R_A/R_1 , 0.93; subsidiary marginal tooth of left mandible with proximal end just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 14.41; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal slightly shorter than that of second, $R_A/R_1.R_m$, 14.80. Fore tibia scarcely swollen, T_1/T_w , 5.05, third apical spur short, about one-quarter length of other two. Mesenteric junction with proctodeum distinctly longer than diagonal; enteric valve nearly sessile on second pouch of proctodeum, dorsolateral in unopened abdomen; enteric valve cushion in position 1 sclerotized throughout its length, half of which protrudes beyond tips of spines of other positions, dilated end fringed with 25-28 (average 26.7) elongated spines, outer half of shaft, and concave surface of dilated end with scattered small spines, base of shaft wrinkled transversely; cushions in other positions with 3-8 (average 5.3) elongated slender slightly curved spines, hooked at tips, but not with completely recurved hooks, and smaller spines on rest of length; membranous wall of valve between and beyond cushions without detectable spicules.



FIGS 454-461. *Ateuchotermes*, imago mandibles, 454, 455, *A. retifaciens*; 456, 457, *A. sentosus*; 458, 459, *A. spinulatus*; 460, 461, *A. tranquillus*.

Measurements (one specimen) in millimetres.

Head width (W)	0.96
Fore tibia width (T_w)	0.14
Fore tibia length (T_l)	0.69
Postclypeus length (Pcl)	0.26
Left mandible, apical to first marginal (L_A)	0.12
Left mandible, first to third marginal (L_1)	0.16
Left mandible, third marginal to molar (L_m)	0.05
Right mandible, apical to first marginal (R_A)	0.11
Right mandible, first to second marginal (R_1)	0.12
Right mandible, second marginal to molar (R_m)	0.06

Comparisons of *A. spinulatus* have already been made with all the other species apart from *A. tranquillus*. This is distinguishable in the imago and worker castes by the shorter apical teeth of the mandibles, the longer outer edge of the right first marginal, in the imago by the vestigial third apical spur of the fore tibia, and in the worker by the distinctive enteric valve.

Holotype queen, paratype nymphs and workers from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Katanga, Keyberg, near Elizabethville, 21.iv.1948 (*A. E. Emerson*) in American Museum of Natural History.

The single nest-series is recorded as from a mound about 1 foot high, 14 inches base diameter, of earth-carton with very thick walls, near the top of a rocky hill in savanna woodland.

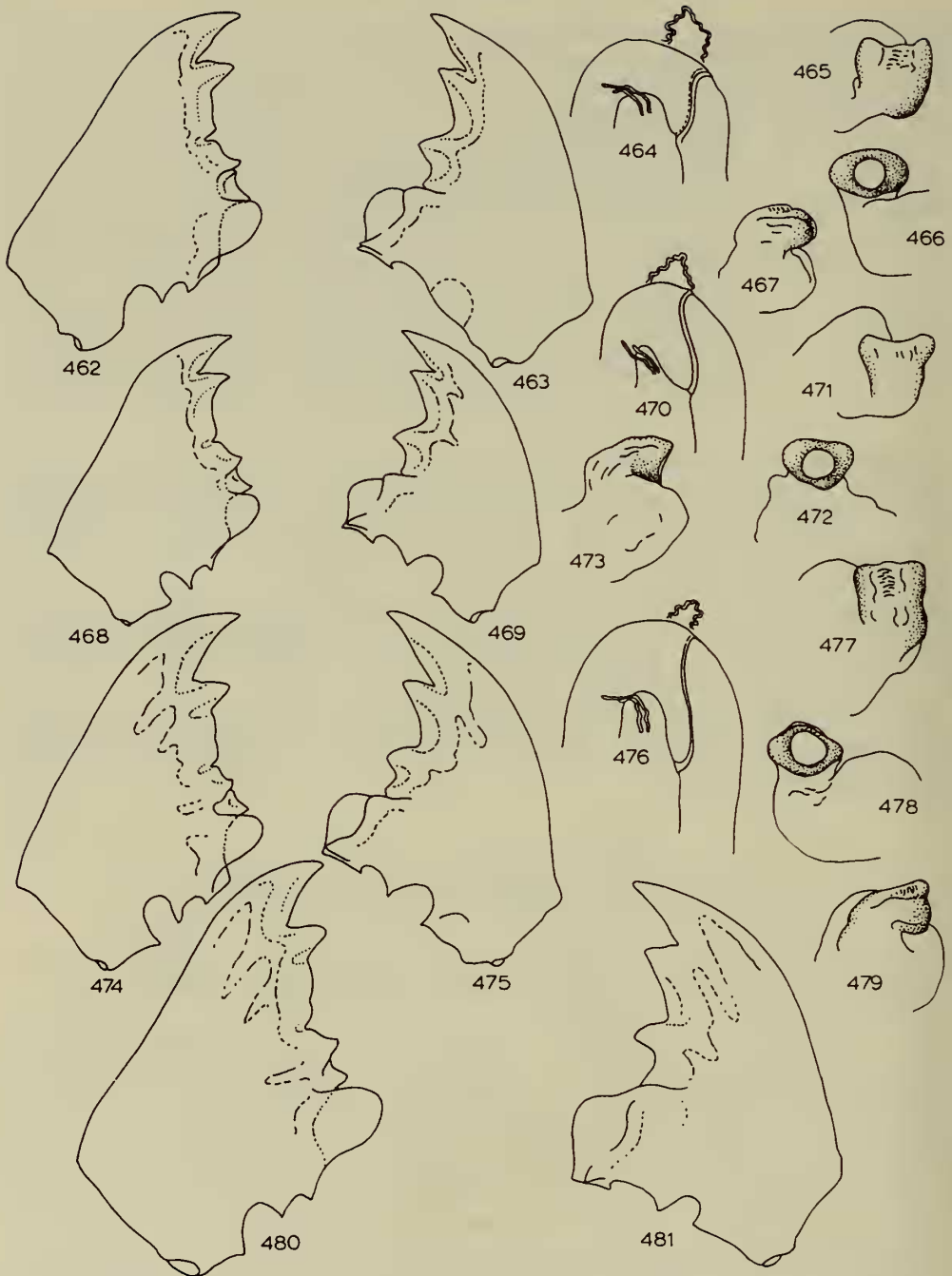
Ateuchotermes tranquillus (Silvestri) **comb. n.**

(Text-figs 452, 453, 460, 461, 480 & 481; Pl. 4, fig. 5)

Anoplotermes tranquillus Silvestri, 1914 : 52. LECTOTYPE ♀, GUINEA: Mamou (Silvestri Coll., Istituto di Entomologia Agraria, Naples) here designated [examined].

Imago. (Old specimens, colour faded in preservation.) Head capsule sepia-brown, darker above ocelli; fontanelle short oval, flat or slightly depressed, sometimes nearly as large as ocellus, slightly paler than head; medial spot short oval, much smaller than fontanelle, flat or slightly raised, coloured as head; postclypeus, sepia-brown, labrum yellow-brown; frontal marks almost flat, shining crescents, slightly paler than head; antennae pale brown. Pronotum, meso- and metanota, sepia-brown, transverse dark sutures distinct; femora brown, tibiae and tarsi, pale brown. Abdominal tergites sepia-brown, sternites brown, paler in middle, dorsal and ventral stigmata darker than sclerites; cerci very pale brown.

Posterior margin of head capsule evenly rounded, ocelli small, separated from compound eyes by nearly one and a half times own least diameter; postclypeus moderately inflated, Pcl/W, 0.29, posterior margin evenly rounded, median suture distinct, apart from anterior one-third. Apical teeth of mandibles short, L_A/L_1 , 0.51, R_A/R_1 , 0.66; subsidiary marginal tooth of left mandible clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 5.33; points of apical and marginal teeth of right mandible in line, anterior edge of first marginal



FIGS 462-481. *Ateuchotermes*, worker mandibles, mesenteric-proctodeal junctions showing attachments of malpighian tubules and positions of malpighian knot, and views of enteric valve seatings. 462-467, *A. retifaciens*; 468-473, *A. sentosus*; 474-479, *A. spinulatus*; 480, 481, *A. tranquillus* (mandibles somewhat worn).

longer than that of second. Meso- and metanota moderately wide at constriction, M/W, 0.30. Pilosity of head capsule forms a slightly uneven pelt with emergent setae. Fore tibia with vestigial third apical spur.

Measurements (one specimen) in millimetres.

Head width across eyes (W)	1.20
Ocellus ($O_w \times O_l$)	0.08 \times 0.11
Ocellus to eye (O-E)	0.11
Postclypeus length (Pcl)	0.35
Antennal article III	0.06
Antennal article IV	0.07
Antennal article V	0.06
Left mandible, apical to first marginal (L_A)	0.10
Left mandible, first to third marginal (L_1)	0.19
Left mandible, third marginal to molar (L_m)	0.10
Right mandible, apical to first marginal (R_A)	0.10
Right mandible, first to second marginal (R_1)	0.15
Right mandible, second marginal to molar (R_m)	0.10
Mesonotum width (M)	0.36
Metanotum width (N)	0.41

Worker. Head capsule pale yellow, pilosity sparse, yellow. Postclypeus weakly inflated, Pcl/W, 0.25. Apical teeth of mandibles short, L_A/L_1 , 0.63, R_A/R_1 , 0.82; subsidiary marginal tooth of left mandible clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 10.41; point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edges of marginals about equal in length, $R_A/R_1.R_m$, 11.00. Fore tibia slender, T_1/T_w , 5.73, third apical spur vestigial, extremely minute. Mesenteric junction with proctodeum diagonal; enteric valve seating connected to second pouch of proctodeum by distinct neck, dorsolateral in unopened abdomen; enteric valve cushion in position 1 only sclerotized on distal half, only about one-quarter of total length of cushion protruding beyond tips of spines of other cushions, dilated end fringed with 13-18 elongated spines, rest of length of cushion including unsclerotized base with small spines; cushions in other positions edged with 5-10 elongated curved spines, very sharply tapered so that tips appear almost blunt, and small spines on remainder of cushion; membranous wall of valve between and beyond cushions with detectable spicules.

Measurements (one specimen) in millimetres.

Head width (W)	1.10
Fore tibia width (T_w)	0.14
Fore tibia length (T_1)	0.79
Postclypeus length (Pcl)	0.27
Left mandible, apical to first marginal (L_A)	0.11
Left mandible, first to third marginal (L_1)	0.18
Left mandible, third marginal to molar (L_m)	0.06
Right mandible, apical to first marginal (R_A)	0.11

Right mandible, first to second marginal (R ₁)	0.14
Right mandible, second marginal to molar (R _m)	0.08

All of the necessary comparisons of *A. tranquillus* have already been made in the discussions on the other species. As indicated in the generic discussion, the enteric valve armature of the workers forms a sequence, and apart from an un-named species known only from the workers and illustrated in Pl. 4, *A. tranquillus* represents the most primitive form.

A lectotype is designated from the existing syntype material as indicated below.

Type-material. *Anoplotermes tranquillus* Silvestri, LECTOTYPE ♀ imago, paralectotype queen, ♂ imago and three workers from type-colony, GUINEA: Mamou, 10°20'N., 12°15'W., 26.viii.1912 (*F. Silvestri*), in Silvestri Coll., Istituto di Entomologia Agraria, Portici, Naples; other paralectotypes in AMNH.

Only the type-series is known.

ANAOROTERMES gen. n.

(An—'without', aoros, Gr., 'weapon')

Type-species: *Anaorotermes echinocolon* sp. n.

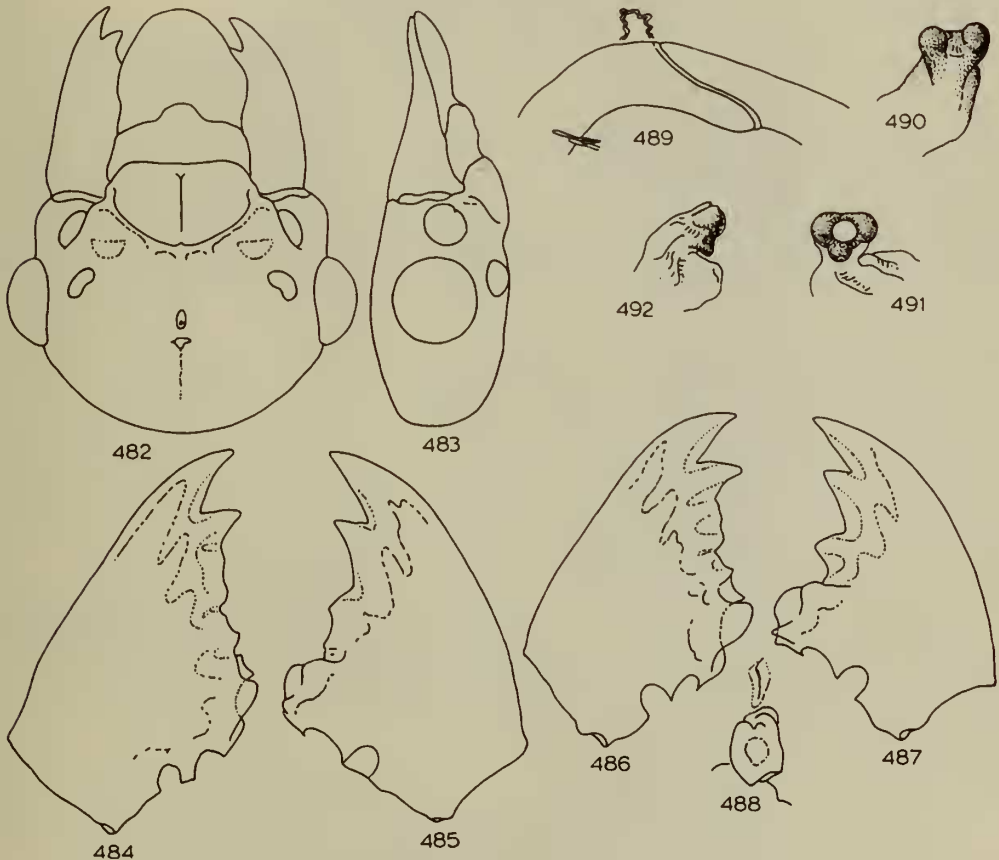
Imago. Large sized, W, 1.11–1.13. Fore tibia with three apical spurs, third well developed. Apical teeth of mandibles short, L_A/L_1 , 0.49–0.51, R_A/R_1 , 0.75–0.81; subsidiary marginal tooth of left mandible with proximal end clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 6.55–7.10; points of apical and marginal teeth of right mandible approximately in line, anterior edges of first and second marginals equal. Meso- and metanota moderately wide at constriction, M/W, 0.31, transverse dark sutures present; complex ratio of mandible and notal measurements, $L_1/M.N$, 1.41–1.55.

Worker. Large sized, W, 0.88. Fore tibia slender, T_1/T_w , 5.89, with three apical spurs, third smaller than other two but not vestigial. Apical teeth of mandibles short, L_A/L_1 , 0.53, R_A/R_1 , 0.80; subsidiary marginal tooth of left mandible with proximal end just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 10.60; point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edge of first marginal slightly shorter than that of second, complex ratio, $R_A/R_1.R_m$, 15.90. Mesenteric junction with proctodeum overlapping, length about twice width of mesenteron at insertion of malpighian tubules, just to right of malpighian knot. Enteric valve seating with two rather prominent outer lobes and a smaller inner lobe, attached to very muscular second pouch of proctodeum by short neck, dorsolateral in position in unopened abdomen; internal cushions of enteric valve different in every position, position 1 vestigial, retracted, unsclerotized, armature at most one or two minute scales or teeth on inner face; position 2, produced slightly through valve opening as one or two elongated sclerotized spines, rest of armature a few minute spines on unsclerotized part of cushion; position 3, distal end of cushion sclerotized, hemispherical, everted through valve opening, and covered with about 35 stout elongated curved spines, rest of cushion unsclerotized, with many small spines; position 4, produced through valve opening, distal end sclerotized with rake-like row of 7–8 elongated outwardly curved spines, rest of cushion unsclerotized, with many small spines.

The enteric valve armature of *Anaorotermes* is almost as bizarre as some of the genus *Ateuchotermes*, and may serve a similar function, though this is achieved in a different manner. The larger bilateral development of position 3 recalls *Alysc-*

termes and some *Anenteotermes*, but the structure is different in many respects. In the analysis of the similarity matrix, *Anaorotermes* comes out next to *Ateuchotermes* by single linkage clustering. Median sorting places it closer to *Aderitotermes*, and when the latent vectors of the principal co-ordinates analysis are examined, it shows relationships to *Alyscotermes*, *Amicotermes* and *Ateuchotermes* in the first six.

In the imago caste, *Anaorotermes* is distinguished from *Ateuchotermes* and *Aderitotermes* by its dense irregular head pilosity which does not form a pelt, and from *Alyscotermes*, *Astalotermes* and *Astratotermes* by its oddly shaped almost triangular fontanelle. *Amicotermes* has longer apical mandibular teeth. It is unlikely to be confused with any other genus. In the worker caste, the enteric valve armature is so distinct and characteristic that no comparisons are necessary.



FIGS 482-492. *Anaorotermes echinocolon*. 482, 483, front and side views of imago head capsule; 484, 485, imago mandibles; 486-488, worker ditto, including surface view of right molar plate; 489, mesenteric-proctodeal junction showing position of malpighian knot and attachment of malpighian tubules; 490-492, views of enteric valve seating.

Anaotermes echinocolon sp. n.

(Text-figs 482-492; Pl. 7, figs 1-3)

Imago. Head capsule sepia-brown, darker above ocelli; fontanelle much smaller than ocellus, flat or slightly depressed, broader than long, irregularly shaped, approximately triangular, very pale brown; medial spot circular, about equal in size to fontanelle, slightly raised, brown; postclypeus brown, labrum pale yellow-brown; frontal marks distinct, flat, semicircular, brown; antennae yellow. Pronotum, meso- and metanota, brown; femora pale yellow-brown, tibiae yellow, tarsi paler. Abdominal tergites brown, dorsal stigmata paler, sternites laterally yellow-brown, ventral stigmata and middle of sternites pale yellow; cerci yellow-white.

Posterior margin of head capsule not quite evenly rounded, slightly undulating; ocelli medium sized, separated from compound eyes by slightly less than own least diameter; postclypeus moderately inflated, Pcl/W, 0.26, posterior margin arched or slightly angular, not evenly rounded, median suture distinct except anterior end. Pilosity of head capsule uneven, not forming a pelt. Other characters given in generic diagnosis.

Measurements (two specimens from one locality) in millimetres.

Head width across eyes (W)	1.11-1.13
Ocellus ($O_w \times O_l$)	0.09-0.10 \times 0.12-0.13
Ocellus to eye (O-E)	0.08
Postclypeus length (Pcl)	0.29
Antennal article III	0.06
Antennal article IV	0.06
Antennal article V	0.06
Left mandible, apical to first marginal (L_A)	0.09
Left mandible, first to third marginal (L_1)	0.18-0.19
Left mandible, third marginal to molar (L_m)	0.07-0.08
Right mandible, apical to first marginal (R_A)	0.10
Right mandible, first to second marginal (R_1)	0.13-0.14
Right mandible, second marginal to molar (R_m)	0.08
Mesonotum width (M)	0.34-0.35
Metanotum width (N)	0.34-0.38

Worker. Head capsule yellow-white, pilosity sparse, pale yellow. Postclypeus moderately inflated, Pcl/W, 0.28. Membranous wall of enteric valve between and beyond cushions without detectable spicules. Other characters given in generic diagnosis.

Measurements (one specimen) in millimetres.

Head width (W)	0.88
Fore tibia width (T_w)	0.11
Fore tibia length (T_1)	0.66
Postclypeus length (Pcl)	0.24
Left mandible, apical to first marginal (L_A)	0.08
Left mandible, first to third marginal (L_1)	0.15
Left mandible, third marginal to molar (L_m)	0.05
Right mandible, apical to first marginal (R_A)	0.09

Right mandible, first to second marginal (R ₁)	0·11
Right mandible, second marginal to molar (R _m)	0·05

Since there is only one species in the genus, all the necessary comparisons are made under the generic heading. It only remains to mention that the abdomen appears to be dehiscent in *A. echinocolon*.

Holotype ♀ imago, paratype ♂ and ♀ imagos and workers from type-colony, NIGERIA: 30 miles from Lokoja on Okene Road (*W. A. Sands*, coll. No. S.2093), in British Museum (Natural History).

The single nest-series was found in an amorphous low earth mound.

ASAGAROTERMES gen. n.

(A—'without', sagaris, Gr., 'A kind of sword')

Type-species: *Asagarotermes coronatus* sp. n.

Imago. Medium-sized, W, 1·03–1·10. Fore tibia with three apical spurs, third almost equal to other two. Apical teeth of mandibles rather long, L_A/L_1 , 0·78–0·80, R_A/R_1 , 1·09–1·18; subsidiary marginal tooth of left mandible with proximal end just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 11·80–12·79; points of apical and marginal teeth of right mandible approximately in line, anterior edge of first marginal slightly longer than that of second, nearly equal. Meso- and metanota narrow at constriction, M/W, 0·20–0·33, transverse dark sutures strongly developed; complex ratio of mandible and notal measurements, $L_1/M.N$, 2·50–4·16.

Worker. Large-sized, W, 0·85–0·88. Fore tibia weakly swollen, T_1/T_w , 4·40–4·49, with three apical spurs, third about half length of other two. Apical teeth of mandibles very long, L_A/L_1 , 0·96–0·99, R_A/R_1 , 1·11–1·16; subsidiary marginal tooth of left mandible with proximal end just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 16·33–22·00; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edges of marginal teeth equal in length, complex ratio, $R_A/R_1.R_m$, 20·60–22·65. Mesenteric junction with proctodeum overlapping by about one and a half times width of mesenteron at insertion of malpighian tubules, anterior end of proctodeum within malpighian knot. Enteric valve seating almost without lobes, practically a rim, sessile on second pouch of proctodeum, lateral in unopened abdomen; internal cushions of enteric valve weakly developed unsclerotized, and unarmed except for a single narrow but strongly sclerotized spiked coronet-like band girdling the middle of each cushion.

This strange type of armature has not been found in any other species, nor has any precursor or even distant relative appeared among the other genera. The spikes on the 'coronet' are more numerous at its outer ends, and appear to engage with those of neighbouring cushions. It is clear from Pl. 7 that this cannot be any kind of filtering device and the only function that suggests itself is a stiffening one, keeping open the lumen of the valve whilst allowing for expansion if needed.

Asagarotermes seems to be equally isolated in the analyses of the similarity matrix to *Apagotermes* and *Amalotermes*, being the penultimate species sorted by single linkage and in the last four by median sorting. The same comments apply to its position on the vector diagrams—it tends to fall in the 'gaps' rather than to be a complete outlier.

In keying out the imago caste, *Asagarotermes* with its narrow meso- and metanotal constrictions comes nearest to *Anenteotermes* and Group I *Astalotermes*. It is larger than nearly all of these and can be distinguished from the one or two largest species by its longer apical mandibular teeth. *Aganotermes*, which combines size, narrow nota and long apical teeth, has the subsidiary marginal tooth of the left mandible level with the edge of the molar prominence, not clear of it as in *Asagarotermes*. It also has a shorter postclypeus and ocelli further from the eyes.

The worker caste of *Asagarotermes* is so distinctive in its enteric valve armature that there is no necessity for detailed comparisons with other genera.

Asagarotermes coronatus sp. n.

(Text-figs 493-502; Pl. 7, figs 4 & 5)

Imago. Head capsule dark sepia-brown, darker above ocelli; fontanelle less than half size of ocellus, oval, slightly depressed, more so at anterior end, coloured as head; medial spot equal to fontanelle or smaller, oval, flat, coloured as head; postclypeus sepia-brown, labrum yellow-brown; frontal marks distinct, semicircular, flat, coloured as head; antennae brown. Pronotum meso- and metanota, sepia-brown; femora brown, tibiae yellow-brown, tarsi yellow. Abdominal tergites brown, dorsal stigmata slightly darker, sternites pale brown, paler in mid-line, ventral stigmata darker. Cerci yellow.

Posterior margin of head capsule evenly rounded; ocelli medium-sized, separated from compound eyes by two-thirds, up to only slightly less than own least diameter; postclypeus moderately inflated, Pcl/W, 0.29-0.31, posterior margin bowed, not evenly rounded, median suture distinct. Pilosity of head capsule dense, uneven, thick setae, not forming a pelt.

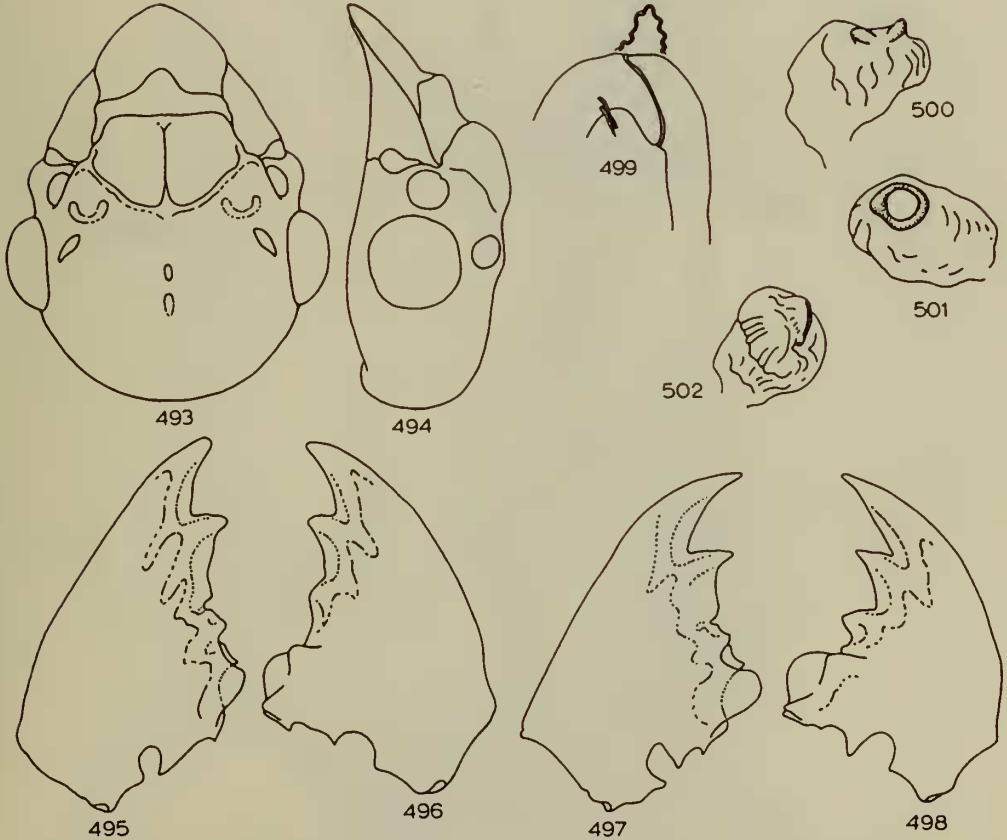
Measurements (three specimens from two nest series) in millimetres.

	Range	Mean
Head width across eyes (W)	1.03-1.10	1.050
Ocellus ($O_w \times O_l$)	0.06-0.08 \times 0.10-0.13	0.07 \times 0.112
Ocellus to eye (O-E)	0.06	0.059
Postclypeus length (Pcl)	0.30-0.33	0.313
Antennal article III	0.05-0.06	0.050
Antennal article IV	0.06-0.07	0.065
Antennal article V	0.06	0.062
Left mandible, apical to first marginal (L_A)	0.12-0.13	0.123
Left mandible, first to third marginal (L_1)	0.16	0.156
Left mandible, third marginal to molar (L_m)	0.06-0.07	0.064
Right mandible, apical to first marginal (R_A)	0.12-0.13	0.123
Right mandible, first to second marginal (R_1)	0.11	0.110
Right mandible, second marginal to molar (R_m)	0.07-0.08	0.075
Mesonotum width (M)	0.20-0.25	0.225
Metanotum width (N)	0.19-0.25	0.221

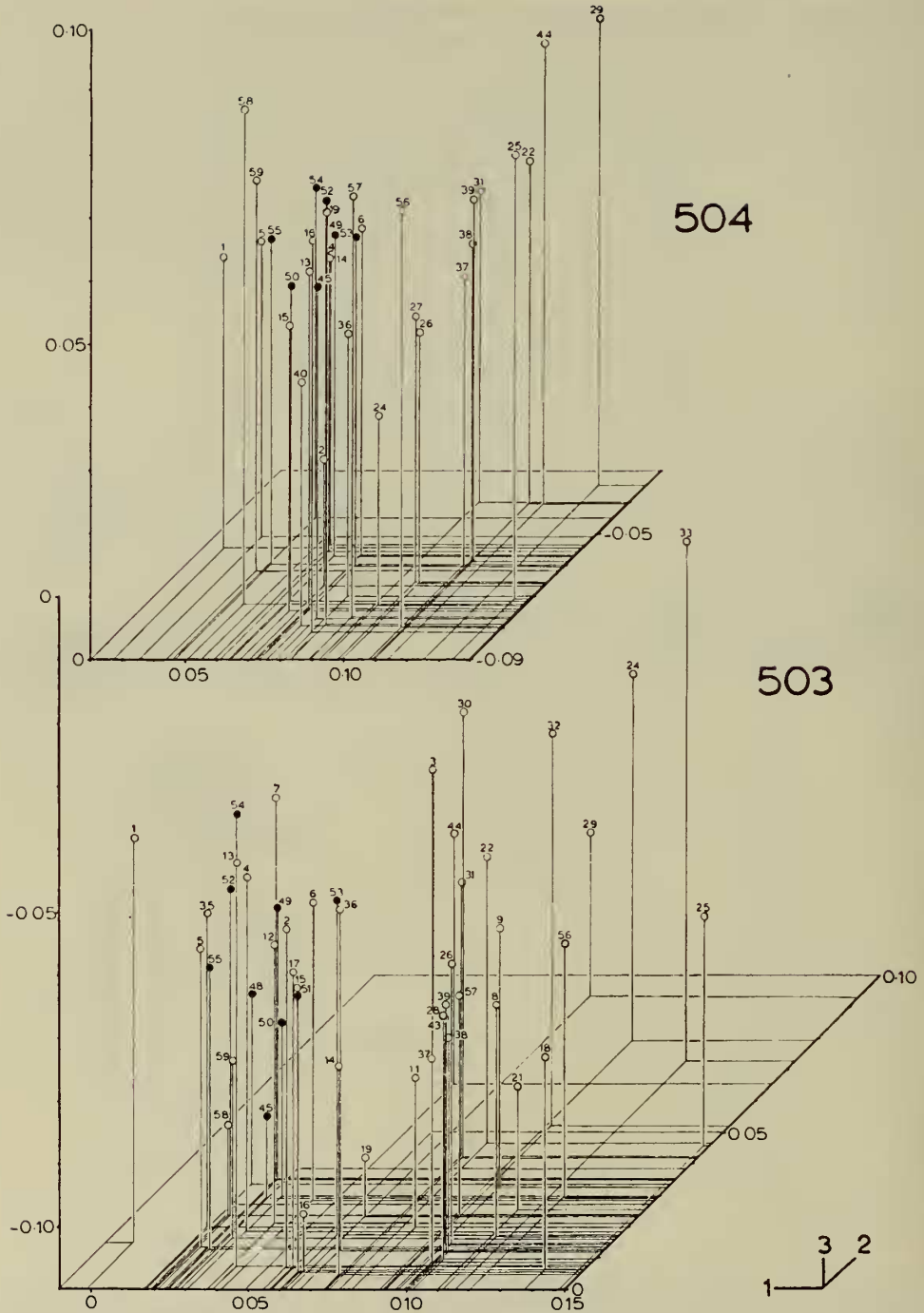
Worker. Head capsule pale yellow to yellow, pilosity yellow to orange-yellow. Postclypeus moderately inflated, Pcl/W, 0.27-0.28. Membranous wall of enteric valve beyond cushions with sparse minute spicules. Other characters given in generic diagnosis.

Measurements (two specimens from two nest series) in millimetres.

Head width (W)	0.85-0.88
Fore tibia width (T_w)	0.13
Fore tibia length (T_l)	0.55-0.58
Postclypeus length (Pcl)	0.24
Left mandible, apical to first marginal (L_A)	0.12
Left mandible, first to third marginal (L_1)	0.13
Left mandible, third marginal to molar (L_m)	0.05-0.06
Right mandible, apical to first marginal (R_A)	0.12
Right mandible, first to second marginal (R_1)	0.10-0.11
Right mandible, second marginal to molar (R_m)	0.05



FIGS 493-502. *Asagarotermes coronatus*. 493, 494, front and side views of imago head capsule; 495, 496, imago mandibles (worn); 497, 498, worker ditto; 499, mesenteric-proctodeal junction showing attachment of malpighian tubules and position of malpighian knot; 500-502, views of enteric valve seating.



FIGS 503 & 504. Three-dimensional graphs of canonical variates 1, 2 & 3 showing species of *Anenteotermes* as solid spots. 503, imago; 504, worker caste.

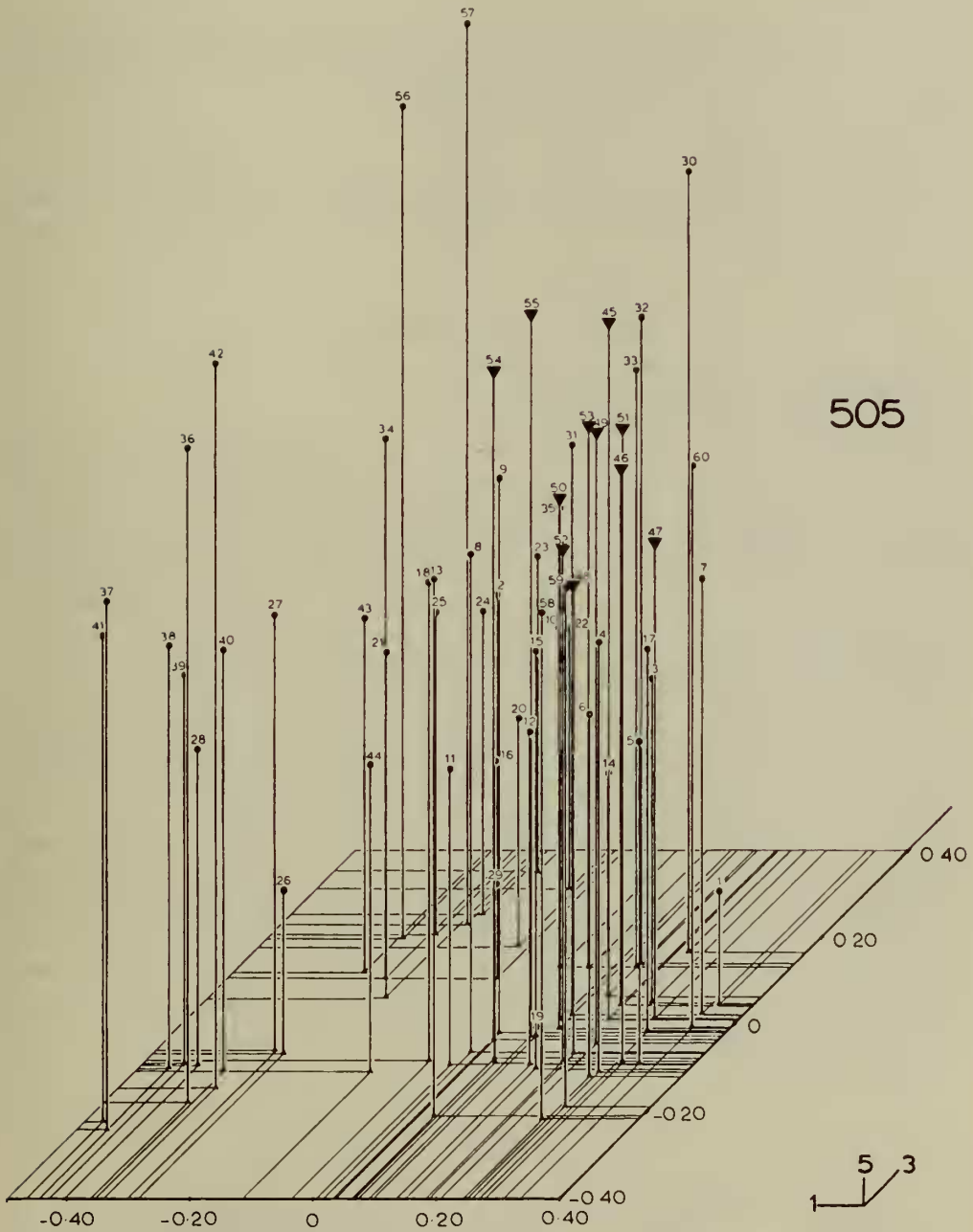


FIG. 505. Three-dimensional graph of principal co-ordinates analysis-plots of eigenvectors 1, 3 and 5 showing species of *Anenteotermes* marked by large triangles.

All the necessary comparisons of the single species are made under the generic heading. It only remains to add that there is no sign of the abdomen being dehiscent in this genus.

Holotype queen, paratype king, and worker from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Katanga, Keyberg, near Elizabethville, 23.iv.1948 (*A. E. Emerson*), in American Museum of Natural History.

Other paratype material. Locality as above: 22.iv.1948 (*A. E. Emerson*), queen and workers, in AMNH.

These nest-series were both collected from *Cubitermes* mounds in seasonally flooded areas 'Dambo' in the typical *Brachystegia-Isobерlinia* woodland of the area.

ANENTEOTERMES gen. n.

(An—'without', enteon, Gr., 'fighting gear')

Type-species: *Anenteotermes disluctans* sp. n.

Imago. Very small, to medium sized, W, 0.65–1.06. Fore tibia with three apical spurs, third well developed. Apical teeth of mandibles short to moderately long, L_A/L_1 , 0.42–0.76, R_A/R_1 , 0.62–1.00; subsidiary marginal tooth of left mandible with proximal end just clear to distinctly clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 6.73–15.92. Right mandible with points of apical and marginal teeth in line, or first marginal retracted behind line from apical to second marginal; anterior edge of first marginal longer than that of second, equal to it, or shorter. Meso- and metanota narrow to fairly wide at constriction, only one species wider, M/W, 0.19–0.31 (0.26), transverse dark sutures usually present but not strongly developed; complex ratio of mandible and notal measurements, $L_1/M.N$, 1.70 (3.11)–5.51 (figures in parentheses represent limits of range excluding single 'unusual' species).

Worker. Very small to medium sized, W, 0.56–0.84. Fore tibia moderately to scarcely swollen, T_1/T_w , 3.58–5.00 with three apical spurs, third smaller than other two, vestigial in only one species. Apical teeth of mandibles short to moderately long, L_A/L_1 , 0.46–0.73, R_A/R_1 , 0.54–0.89; subsidiary marginal tooth of left mandible with proximal end just clear of molar prominence to widely separated in surface view, complex ratio, $L_A/L_1.L_m$, 9.15–18.52. Right mandible with point of first marginal slightly to distinctly behind line from apical to second marginal; anterior edge of first marginal equal to or shorter than that of second, usually shorter, complex ratio, $R_A/R_1.R_m$, 11.61–21.60. Mesenteric junction with proctodeum overlapping, elongated to form a distinct mixed segment, proximal end of proctodeum well to left of malpighian knot. Enteric valve seating weakly two- or three-lobed, third usually smaller, sessile or with short neck connecting it to second pouch of proctodeum, lateral to dorsolateral in unopened abdomen; internal cushions of enteric valve retracted or produced through valve opening, sometimes elongated and sclerotized, surfaces scaly or armed with small to elongated spines, the latter sometimes pectinate.

The most important distinguishing feature of this genus is the mixed segment of the worker gut. This character is only found in this highly developed form in two other genera, namely *Aderitotermes* and *Adaiphrotermes*. In the latter case the swollen termination of the mesenteron and lack of a third spur on the fore tibia are diagnostic. *Aderitotermes* is larger, and the mixed segment is longer. The enteric valve seating has three prominent and equal lobes and is far dorsal in position in the unopened abdomen. Nevertheless, there is probably a distinct relationship

between these two genera, *Aderitotermes* possibly being a specialized derivative from the same stem as *Anenteotermes*.

Anenteotermes itself contains a wide range of forms, some of them highly specialized in other ways. The armature of the enteric valve again shows a series of developing complexity, not so complete as that seen in *Ateuchotermes* but with enough stages to clearly show the relationship of the simpler to the more advanced forms, which were at first placed in a separate genus.

Although *Anenteotermes* forms an acceptable genus by conventional taxonomic standards, its position in the analysis of the similarity matrix is not so clear. This results very largely from the coding adopted, which treats the length of the mesenteric overlap with the proctodeum as a single multistate quantitative character. This feature is thereby weighted far below what I now consider to be its true significance. This problem is discussed in the sections on numerical taxonomy and phylogeny, but its result is to place *Anenteotermes* very close to *Astalotermes* and *Acholotermes* in the vector diagrams (Text-figs 504-505). It forms a cluster of points which scarcely overlaps with these genera but several points have their nearest neighbour outside this group. Consequently when the clustering is analysed either by single linkage or median sorting, some of the species of *Anenteotermes* are scattered among those of the other genera. This reflects a genuine, very great general similarity in characters other than the mixed segment and enteric valve armature. It is not possible to key out the imago castes of *Anenteotermes* separately from those of *Astalotermes* Group I. It seems likely that *Anenteotermes* was derived from forms resembling *Astalotermes*.

Within the genus *Anenteotermes*, as in *Astalotermes*, the species fall into natural groupings which are also indicated in the cluster analyses. However, in *Anenteotermes* they include fewer species and depend very largely on the degree of development of the enteric valve. There is little to be gained in describing the genus by sorting the species under group headings. It is sufficient to note that the main grouping consists of five species, *A. ateuchestes*, *A. cicur*, *A. disluctans*, *A. hemerus* and *A. improcinctus* in which the mixed segment is fully developed and the enteric valve is without armature other than scales. A second group is formed by *A. amachus* and *A. nanus* in which the enteric valve has spines on the edges of the scales, more developed in the latter species. The third group consists of *A. cnaphorus* and *A. polyscolus* in which the enteric valve armature is most highly developed. There remains *A. improelatans* which should perhaps have come first since it has a shorter mixed segment and the first marginal teeth of imago and worker right mandibles are not appreciably reduced; it also has wider meso- and metanota. These characters would appear to be primitive and to link it with other genera.

KEYS TO SPECIES

Imagos

- | | | |
|---|---|---|
| 1 | Right mandible with anterior edge of first marginal tooth distinctly shorter than that of second marginal | 2 |
| - | Right mandible with anterior edge of first marginal at least as long as that of second | 3 |

- 2 Small, W, 0.65-0.69. Apical teeth of mandibles longer, L_A/L_1 , 0.67-0.76, R_A/R_1 , 0.84-1.00. Postclypeus more inflated, Pcl/W , 0.29-0.32. Fontanelle very small and indistinct, little paler than head **nanus** (p. 215)
- Larger, W, 0.80. Apical teeth of mandibles shorter, L_A/L_1 , 0.54, R_A/R_1 , 0.68. Postclypeus less inflated, Pcl/W , 0.26. Fontanelle more conspicuous, pale, contrasting with head colour **ateuchestes** (p. 198)
- 3 Meso- and metanota proportionately wider at constriction, M/W , 0.28-0.31. Right mandible with anterior edge of first marginal tooth distinctly longer than that of second **improelatus** (p. 212)
- Meso- and metanota proportionately narrower at constriction, M/W , 0.19-0.26. Right mandible with anterior edges of first and second marginals equal 4
- 4 Postclypeus less inflated, Pcl/W , 0.25-0.26 5
- Postclypeus more inflated, Pcl/W , 0.28-0.34 7
- 5 Smaller, W, 0.69-0.79 **polyscolus** (p. 217)
- Larger, W, 0.87-1.06 6
- 6 Larger, W, 0.99-1.06. Postclypeus with sinuate posterior margin and distinct median suture **hemerus** (p. 209)
- Smaller, W, 0.87-0.94. Postclypeus with more or less evenly rounded but indistinct posterior margin, median suture very indistinct or absent **cicur** (p. 200)
- 7 Posterior margin of head capsule behind eyes evenly rounded 8
- Posterior margin of head capsule behind eyes unevenly rounded, slightly undulating **amachetus** (p. 195)
- 8 Smaller, W, 0.69-0.79 9
- Larger, W, 0.84-0.96 10
- 9 Fontanelle minute, vestigial, only slightly paler than head. Pilosity of head capsule dense, uneven, not forming a pelt. Postclypeus generally more inflated, Pcl/W , 0.30-0.34 **improcinctus** (p. 212)
- Fontanelle large, often approaching size of ocelli, usually distinctly paler than head but still visible even when coloured as head. Pilosity often even, forming a pelt with emergent setae. Postclypeus less inflated, Pcl/W , 0.23-0.31 **polyscolus** (p. 217)
- 10 Apical teeth of mandibles longer, L_A/L_1 , 0.60-0.64, R_A/R_1 , 0.83-0.89. (Complex ratios give clearer separation, $L_A/L_1.L_m$, 9.93-10.10, $R_1/R_A.R_m$, 17.3-19.4) **cnaphorus** (p. 203)
- Apical teeth of mandibles shorter, L_A/L_1 , 0.46-0.56, R_A/R_1 , 0.62-0.75 ($L_A/L_1.L_m$, 6.76-8.51, $R_1/R_A.R_m$, 22.0-28.5) **disluctans** (p. 206)

Workers

- 1 Enteric valve cushions armed with distinct spines at their distal ends 2
- Enteric valve cushions not so armed. 4
- 2 Enteric valve cushions in position 3 elongated, protruding through valve opening, armed with a fringe of long pectinate spines, other cushions short, with small spines 3
- Enteric valve cushions not elongated or protruding through valve opening, armed with small spines. **nanus** (p. 215)
- 3 Enteric valve cushions of position 3 shorter and broader as in Pl. 8, fig. 3. Larger, W, 0.72-0.73. Apical teeth of mandibles longer, L_A/L_1 , 0.64-0.66, R_A/R_1 , 0.84-0.89 **cnaphorus** (p. 203)
- Enteric valve cushions of position 3 longer and narrower as in Pl. 8, figs 4-6. Smaller W, 0.60-0.64. Apical teeth of mandibles shorter, L_A/L_1 , 0.50-0.60, R_A/R_1 , 0.68-0.80 **polyscolus** (p. 217)
- 4 Right mandible with anterior edges of first and second marginal teeth equal in length. Mixed segment with proctodeal overlap relatively short, length less

- than three times width of mesenteron at insertion of malpighian tubules, proximal end only just to left of malpighian knot *improelatus* (p. 212)
- Right mandible with anterior edge of first marginal tooth distinctly shorter than that of second. Mixed segment, length of proctodeal overlap more than three times width of mesenteron, proximal end well to left of malpighian knot 5
- 5 Larger, W, 0.84. Postclypeus less inflated, Pcl/R₁, 1.61 *hemerus* (p. 209)
- Smaller, W, 0.61–0.75. Postclypeus more inflated, Pcl/R₁, 1.63–3.00 6
- 6 Apical teeth of mandibles longer, L_A/L₁, 0.61–0.70, R_A/R₁, 0.77–0.84. Smaller, W, 0.60–0.63 7
- Apical teeth of mandibles shorter, L_A/L₁, 0.46–0.53, R_A/R₁, 0.54–0.65. Larger, W, 0.68–0.75 8
- 7 Fore tibia scarcely inflated, T₁/T_w, 5.00, with third apical spur vestigial, one-fifth or less of length of other two. Enteric valve, seating weakly three-lobed, third smaller; connected to second pouch of proctodeum by distinct neck
- amachus* (p. 195)
- Fore tibia inflated, T₁/T_w, 3.85–4.00 with third apical spur distinct, one-quarter or more of length of other two. Enteric valve seating almost a rim, very weakly two-lobed, sessile on second pouch of proctodeum, without a neck
- improcinctus* (p. 210)
- 8 Pilosity of head capsule distinctly darker, conspicuous against paler head *cicur* (p. 200)
- Pilosity of head capsule, fine, pale, inconspicuous 9
- 9 Gambia, West Africa *ateuchestes* (p. 198)
- Central Africa to Uganda *disluctans* (p. 206)

Anenteotermes amachus sp. n.

(Text-figs 506–509 & 518–523; Pl. 8, fig. 1)

Imago. Head capsule brown (queen, colours may be faded), darker above ocelli; fontanelle small, less than half size of ocellus, nearly flat, slightly ridged oval, pale yellow-brown; medial spot circular, smaller than fontanelle, flat, coloured as head; postclypeus yellow-brown, labrum yellow; frontal marks, indistinct flat yellow-brown crescents; antennae, yellow-brown. Pronotum, meso- and metanota yellow-brown, transverse sutures present; femora and tibiae pale yellow-brown, tarsi yellow. Abdominal tergites and dorsal stigmata yellow-brown, sternites and ventral stigmata pale yellow-brown, sternites paler in middle, cerci yellow.

Posterior margin of head capsule slightly undulating, not evenly rounded; ocelli medium-sized, separated from compound eyes by less than half own least diameter; postclypeus moderately inflated, Pcl/W, 0.28, posterior margin evenly rounded, median suture present but weakly developed at each end. Apical teeth of mandibles short, L_A/L₁, 0.57, R_A/R₁, 0.87; subsidiary marginal tooth of left mandible widely clear of molar prominence in surface view, complex ratio, L_A/L₁.L_m, 11.46; point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edges of marginal teeth approximately equal, complex ratio, R₁/R_A.R_m (note difference from ratio used in worker caste), 21.30. Pilosity of head capsule dense, slightly uneven, brown, nearly forming a rough pelt with emergent setae.

Measurements (unique queen) in millimetres.

Head width across eyes (W)	0.80
Ocellus (O _w × O ₁)	0.08 × 0.10
Ocellus to eye (O–E)	0.03
Postclypeus length (Pcl)	0.23
Antennal article III	0.02
Antennal article IV	0.04
Antennal article V	0.04

Left mandible, apical to first marginal (L_A)	0.07
Left mandible, first to third marginal (L_1)	0.13
Left mandible, third marginal to molar (L_m)	0.05
Right mandible, apical to first marginal (R_A)	0.08
Right mandible, first to second marginal (R_1)	0.09
Right mandible, second marginal to molar (R_m)	0.05
Mesonotum width (M)	0.20
Metanotum width (N)	0.20

Worker. Head capsule and pilosity yellow, setae sparse. Postclypeus moderately inflated, Pcl/W , 0.29, Pcl/R_1 , 2.26. Apical teeth of mandibles fairly short, L_A/L_1 , 0.70, R_A/R_1 , 0.84; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio, $L_A/L_1.L_m$, 18.10; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal shorter than that of second. $R_A/R_1.R_m$, 21.60. Fore tibia scarcely swollen, T_1/T_w , 5.00, third apical spur vestigial, less than one-fifth length of other two. Mesenteric overlap with proctodeum about three times as long as width of mesenteron at insertion of malpighian tubules; enteric valve seating with two weakly developed opposed lobes and a smaller third inner lobe, connected to second pouch of proctodeum by a distinct neck, dorsolateral in unopened abdomen; internal cushions of enteric valve all retracted, about equally developed, with scaly surface, posterior margin of each scale with one or more minute points; membranous wall of valve between and beyond cushions with rather numerous minute spicules arranged in curved rows.

Measurements (one specimen) in millimetres.

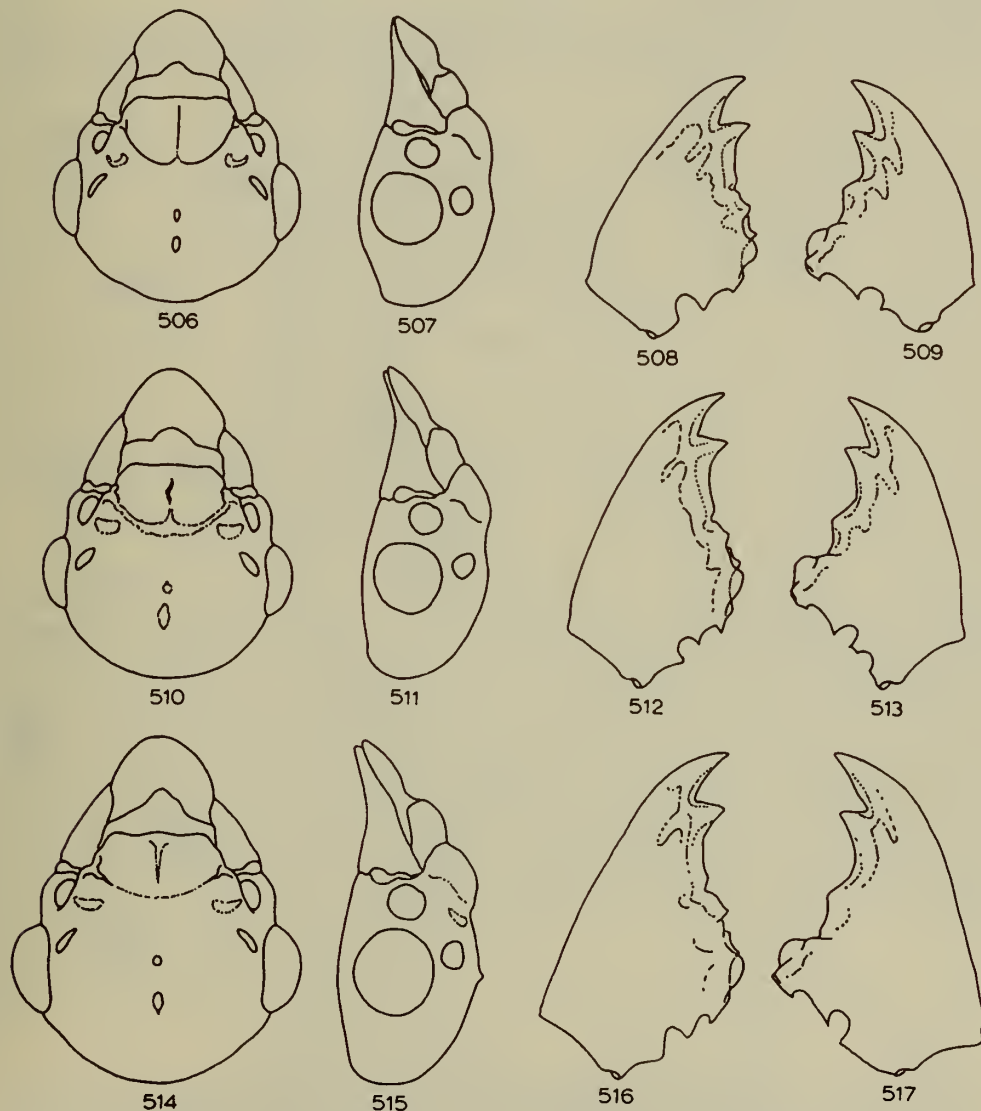
Head width (W)	0.61
Fore tibia width (T_w)	0.09
Fore tibia length (T_1)	0.44
Postclypeus length (Pcl)	0.18
Left mandible, apical to first marginal (L_A)	0.07
Left mandible, first to third marginal (L_1)	0.10
Left mandible, third marginal to molar (L_m)	0.04
Right mandible, apical to first marginal (R_A)	0.07
Right mandible, first to second marginal (R_1)	0.08
Right mandible, second marginal to molar (R_m)	0.04

In the imago caste, *A. amachetus* is one of three species in which the back of the head behind the eyes is not evenly rounded. Of the other two species, *A. cicur* has shorter mandibular apical teeth, a less inflated postclypeus with very indistinct median suture and posterior margin, and a distinctly raised medial spot; *A. improelatanus* has wider meso- and metanotal constrictions. In the worker caste, the vestigial third apical spur on the scarcely swollen fore tibia of *A. amachetus* is diagnostic. The spines of the enteric valve armature further distinguish

A. cnaphorus, *A. nanus* and *A. polyscolus*; the complete lack of points on the scales also separate the other species. The abdomen of the worker caste is dehiscent in *A. amachetus*.

Holotype queen and paratype workers from type-colony, DEMOCRATIC REPUBLIC OF CONGO: 18 km S. of Kinshasa, near Riflart, 9.vi.1948 (*A. E. Emerson*), in American Museum of Natural History.

There is no biological information on this species.



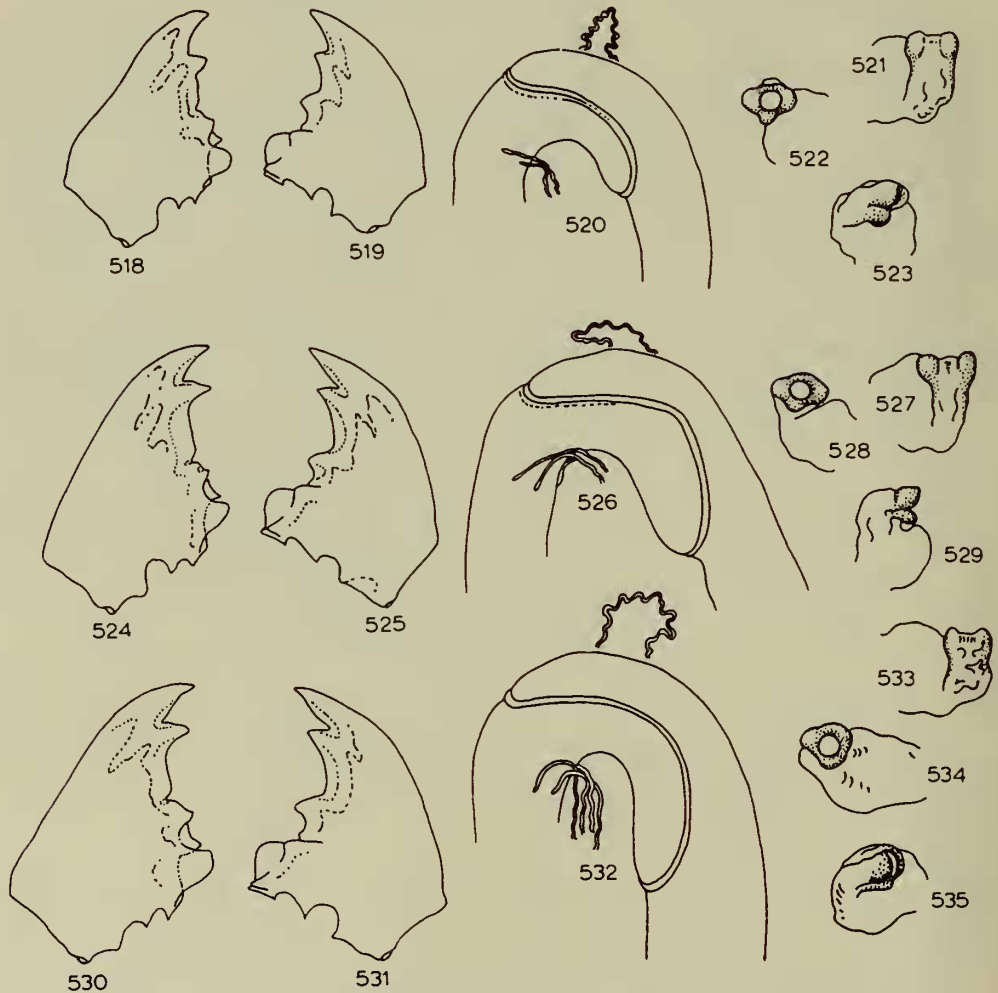
FIGS 506-517. *Anenteotermes*, imago head capsule, front and side views, and imago mandibles. 506-509, *A. amachetus*; 510-513, *A. ateuchestes* ♂; 514-517, *A. cicur*.

Anenteotermes ateuchestes sp. n.

(Text-figs 510-513 & 524-529; Pl. 7, fig. 6)

Imago. Head capsule sepia-brown, darker above ocelli; fontanelle oval, flat, about half size of ocellus, yellow, conspicuous; medial spot short oval, flat or slightly raised, smaller than fontanelle, coloured as head; postclypeus brown, labrum yellow-brown; frontal marks flat brown crescents; antennae pale brown. Pronotum brown, meso- and metanota pale brown, transverse sutures weakly developed; femora pale yellow brown, tibiae and tarsi yellow. Abdominal tergites and sternites pale brown, sternites yellow-white in middle, dorsal and ventral stigmata pale; cerci yellow.

Posterior margin of head capsule evenly rounded, ocelli medium-sized, separated from compound eyes by about two-thirds own least diameter; postclypeus moderately inflated,



FIGS 518-535. *Anenteotermes*, worker mandibles, mesenteric-pectoral junctions showing attachments of malpighian tubules and positions of malpighian knot, and views of enteric valve seatings. 518-523, *A. amachetus*; 524-529, *A. ateuchestes*; 530-535, *A. cicur*.

Pcl/W, 0.26, posterior margin indistinct but more or less evenly rounded, median suture weakly developed. Apical teeth of mandibles short, L_A/L_1 , 0.54, R_A/R_1 , 0.68; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 9.97; points of apical and marginal teeth of right mandible approximately in line, anterior edge of first marginal distinctly shorter than that of second, complex ratio, $R_1/R_A.R_m$ (note difference from ratio used in worker caste), 28.0. Pilosity of head capsule short, dense, uneven, yellow-brown, not forming a pelt.

Measurements (one specimen) in millimetres.

Head width across eyes (W)	0.80
Ocellus ($O_w \times O_1$)	0.07 \times 0.10
Ocellus to eye (O-E)	0.04
Postclypeus length (Pcl)	0.21
Antennal article III	0.04
Antennal article IV	0.05
Antennal article V	0.05
Left mandible, apical to first marginal (L_A)	0.08
Left mandible, first to third marginal (L_1)	0.14
Left mandible, third marginal to molar (L_m)	0.05
Right mandible, apical to first marginal (R_A)	0.08
Right mandible, first to second marginal (R_1)	0.11
Right mandible, second marginal to molar (R_m)	0.05
Mesonotum width (M)	0.18
Metanotum width (N)	0.18

Worker. Head capsule yellow-white, pilosity fine, short, fairly numerous, pale yellow. Postclypeus rather strongly inflated, Pcl/W, 0.32, Pcl/ R_1 , 2.07. Apical teeth of mandibles short, L_A/L_1 , 0.49, R_A/R_1 , 0.61; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 10.89; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal shorter than that of second, $R_A/R_1.R_m$, 15.80. Fore tibia scarcely swollen, T_1/T_w , 4.59, third apical spur about half length of other two, but pale and hard to see. Mesenteric overlap with proctodeum about four times as long as width of mesenteron at insertion of malpighian tubules; enteric valve seating with two moderately developed opposed lobes and a smaller third inner lobe, connected to second pouch of proctodeum by a short neck, lateral in unopened abdomen; internal cushions of enteric valve all retracted, about equally developed, with scaly surface only; membranous wall of valve between and beyond cushions with sparse minute spicules.

Measurements (one specimen) in millimetres.

Head width (W)	0.69
Fore tibia width (T_w)	0.11
Fore tibia length (T_1)	0.49
Postclypeus length (Pcl)	0.22
Left mandible, apical to first marginal (L_A)	0.06
Left mandible, first to third marginal (L_1)	0.13
Left mandible, third marginal to molar (L_m)	0.05

Right mandible, apical to first marginal (R _A)	0·07
Right mandible, first to second marginal (R ₁)	0·11
Right mandible, second marginal to molar (R _m)	0·04

The short first marginal tooth of the right mandible is used in the key to the imago caste to characterize *A. ateuchestes* and *A. nanus*. It is difficult to use in that this tooth wears more readily than the second marginal and so produces a similar appearance in some other species in which it is normally about equal to the second. Thus in the imago a large specimen of *A. polyscolus* with worn mandibles may be very like *A. ateuchestes*. The head pilosity of the latter is uneven, not forming a pelt, whereas *A. polyscolus* has a very even pelt in most of its range. Other species in which the mandible character may break down are *A. amachetus*, which has already been discussed under its own heading; and *A. cnaphorus* which is larger, found in Southern Congo, and has an inconspicuous fontanelle. *A. nanus* keys out with *A. ateuchestes*, but is much smaller, with longer apical teeth and an indistinct fontanelle.

In the worker caste, the spiny enteric valve armature distinguishes *A. cnaphorus*, *A. nanus* and *A. polyscolus*. *A. improelatus* is larger with a shorter mixed segment. *A. hemerus* is much larger. *A. improcinctus* is smaller with longer mandibular apical teeth. *A. cicur* has more conspicuous head capsule setae. *A. disluctans* is indistinguishable except for a very slightly more swollen fore tibia, but is East and Central African in distribution. The abdomen of the worker appears to be dehiscent in *A. ateuchestes*.

Holotype ♂ imago, three paratype ♂ imagos and workers from type-colony, GAMBIA: 11 m. from Bathurst on Yundum Road, 12.ix.1966 (*W. A. Sands*, coll. No. S.2848) in British Museum (Natural History).

The single nest-series was found in a wide, rather flat, fairly hard mound without well defined structure on dark sandy grey soil in open bush.

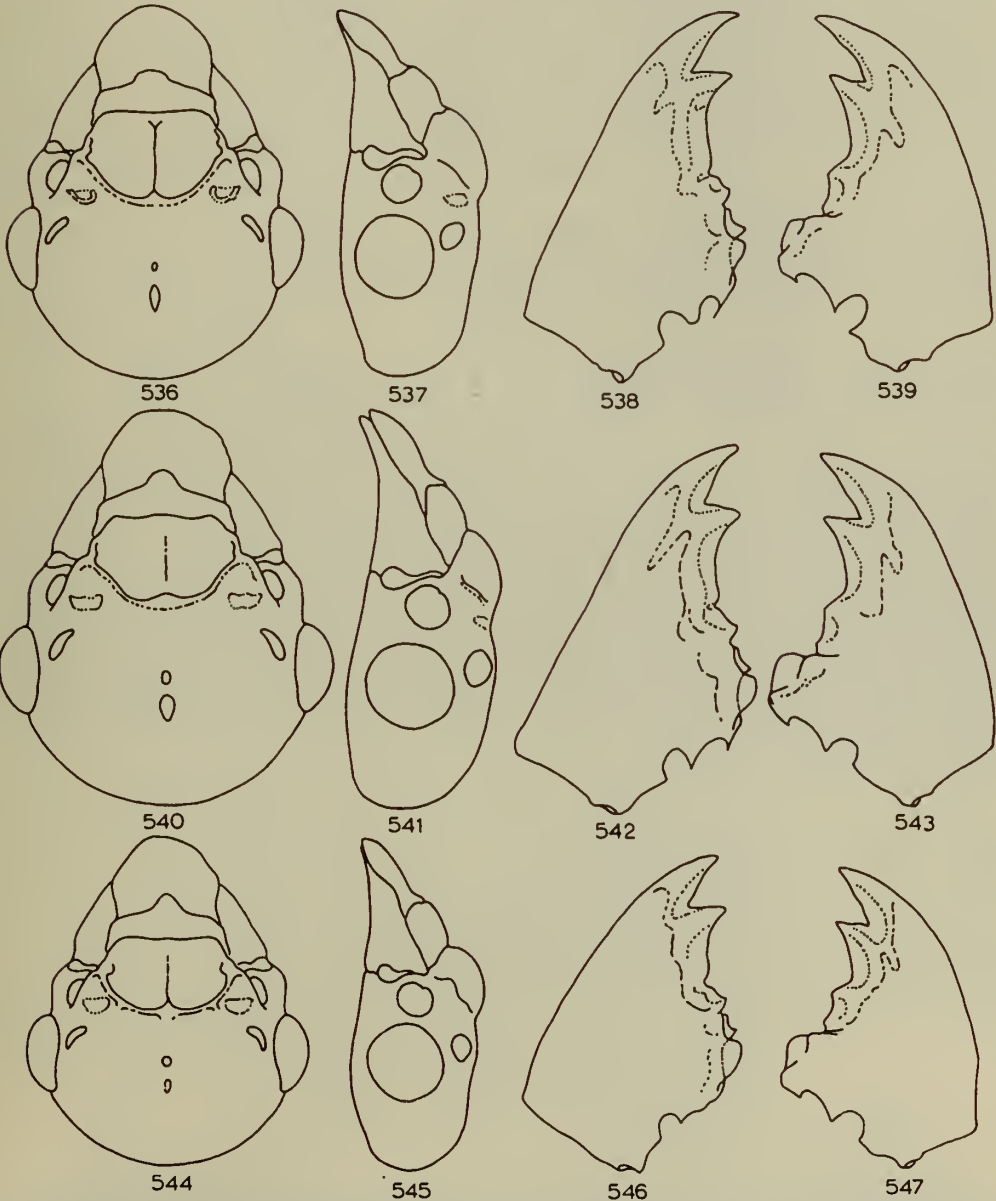
Anenteotermes cicur sp. n.

(Text-figs 514-517 & 530-535)

Imago. Head capsule dark sepia-brown, darker above ocelli; fontanelle about half size of ocellus, oval, slightly depressed, pale brown; medial spot short oval, half as large as fontanelle, slightly but distinctly raised into small bump clearly visible in profile, sepia-brown; postclypeus sepia-brown, labrum brown; frontal marks flat sepia-brown crescents; antennae yellow-brown. Pronotum sepia-brown, meso- and metanota brown, transverse suture absent on meso-, weakly developed on metanotum; femora and tibiae pale yellow-brown, tarsi yellow. Abdominal tergites sepia-brown, dorsal stigmata darker; sternites yellow-brown, paler in middle, ventral stigmata sepia-brown; cerci yellow.

Posterior margin of head capsule slightly undulating, not evenly rounded; ocelli medium-sized, separated from compound eyes by less than half up to two-thirds own least diameter; postclypeus rather weakly inflated, Pcl/W, 0·25-0·26, posterior margin somewhat indistinct, widely rounded, median suture almost absent, apical teeth of mandibles short, L_A/L₁, 0·49-0·50,

R_A/R_1 , 0.70; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 6.73-7.33; point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edges of marginal teeth approximately equal, complex ratio, $R_1/R_A.R_m$ (note difference from ratio used in worker caste), 21.6-22.9. Pilosity of head capsule uneven, brown, not forming a pelt.



FIGS 536-547. *Anenteotermes*, imago head capsule, front and side views, and imago mandibles. 536-539, *A. disluctans*; 540-543, *A. hemerus*; 544-547, *A. improelatanans*.

Measurements (two specimens from one nest series) in millimetres.

Head width across eyes (W)	0.87-0.94
Ocellus ($O_w \times O_l$)	0.07-0.08 \times 0.09-0.10
Ocellus to eye (O-E)	0.03-0.05
Postclypeus length (Pcl)	0.23-0.24
Antennal article III	0.04-0.05
Antennal article IV	0.04-0.05
Antennal article V	0.04-0.05
Left mandible, apical to first marginal (L_A)	0.08
Left mandible, first to third marginal (L_1)	0.15-0.16
Left mandible, third marginal to molar (L_m)	0.07
Right mandible, apical to first marginal (R_A)	0.09
Right mandible, first to second marginal (R_1)	0.13
Right mandible, second marginal to molar (R_m)	0.06-0.07
Mesonotum width (M)	0.19-0.21
Metanotum width (N)	0.18-0.21

Worker. Head capsule pale yellow, pilosity yellow, setae fairly numerous though not dense. Postclypeus moderately inflated, Pcl/W, 0.28, Pcl/ R_1 , 1.79. Apical teeth of mandibles short, L_A/L_1 , 0.46, R_A/R_1 , 0.58; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 9.15; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal about half as long as that of second, $R_A/R_1.R_m$, 13.52. Fore tibia weakly swollen, T_1/T_w , 4.12, third apical spur about half length of other two. Mesenteric overlap with proctodeum about four times as long as width of mesenteron at insertion of malpighian tubules; enteric valve seating with three very weakly developed lobes connected to second pouch of proctodeum by a distinct neck, lateral in unopened abdomen; internal cushions of enteric valve all retracted, about equally developed, with scaly surface; membranous wall of valve between and beyond cushions with sparse minute spicules.

Measurements (one specimen) in millimetres.

Head width (W)	0.74
Fore tibia width (T_w)	0.13
Fore tibia length (T_1)	0.53
Postclypeus length (Pcl)	0.21
Left mandible, apical to first marginal (L_A)	0.06
Left mandible, first to third marginal (L_1)	0.14
Left mandible, third marginal to molar (L_m)	0.05
Right mandible, apical to first marginal (R_A)	0.07
Right mandible, first to second marginal (R_1)	0.12
Right mandible, second marginal to molar (R_m)	0.04

As already stated under *A. amachetus*, the imago caste of *A. cicur* is one of three species in which the back of the head behind the eyes is not evenly rounded. The

remaining species, *A. improelatus*, has wider meso- and metanotal constrictions, longer mandibular apical teeth, and the right first marginal tooth longer than the second. In the worker caste, it has already been compared with *A. amachus* and *A. atechestes*. It is distinguished from *A. cnaphorus*, *A. nanus* and *A. polyscolus* by its unarmed enteric valve. *A. improelatus* is distinguished by the equal length of the anterior edges of first and second marginal teeth of the right mandible, and the much shorter mixed segment. The latter feature is also shorter in *A. hemerus*, though not as short as in the previously mentioned species. *A. hemerus* is also larger with less inflated postclypeus. *A. improcinctus* is smaller, with longer mandibular apical teeth, and *A. disluctans* has less conspicuous head setae. The abdomen of the worker caste is not strongly dehiscent in *A. cicur*, only about one in four preserved specimens having burst.

Holotype ♀ imago, paratype ♂ and ♀ imagos and workers from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Yase, 12 km from Yangambi, 31.v.1948 (*A. E. Emerson*), in American Museum of Natural History (paratypes from type-colony also in BMNH).

Other paratype material. DEMOCRATIC REPUBLIC OF CONGO: Kivu, Irangi, 1°53'S., 28°28'E., 5.xi.1963 (*E. Ernst*) in Swiss Tropical Institute, Basle and BMNH.

There is no biological information on this species.

Anenteotermes cnaphorus sp. n.

(Text-figs 566, 575-578 & 595-600; Pl. 8, fig. 3)

Imago. Head capsule sepia-brown (queens, colours may be faded) darker above ocelli; fontanelle elongate oval, irregular in outline, somewhat indistinct, being covered with setae, equal in size to ocelli, or slightly smaller, slightly depressed, brown; medial spot oval, nearly flat, very small, coloured as head; postclypeus brown, labrum yellow-brown; frontal marks indistinct slightly depressed brown crescents; antennae yellow-brown. Pronotum, brown, meso- and metanota yellow-brown, transverse sutures present; femora and tibiae pale yellow-brown, tarsi yellow. Abdominal tergites brown, sternites yellow-brown laterally, yellow in middle, stigmata coloured as sclerites; cerci yellow.

Posterior margin of head capsule evenly rounded; ocelli medium-sized, separated from compound eyes by less than half own least diameter; postclypeus moderately inflated, Pcl/W, 0.29-0.31, posterior margin somewhat irregularly arched, median suture present. Apical teeth of mandibles short, L_A/L_1 , 0.60-0.64, R_A/R_1 , 0.83-0.89; subsidiary marginal tooth of left mandible widely clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 9.93-10.10; point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edges of marginal teeth approximately equal, complex ratio, $R_1/R_A.R_m$ (note difference from ratio used in worker caste), 17.30-19.40. Pilosity of head capsule dense, fairly even, forming a rough pelt with many emergent setae, yellow-brown.

Measurements (three specimens from two localities) in millimetres.

	Range	Mean
Head width across eyes (W)	0.84-0.88	0.865
Ocellus ($O_w \times O_l$)	0.07-0.08 × 0.10-0.11	0.073 × 0.107
Ocellus to eye (O-E)	0.03-0.04	0.033
Postclypeus length (Pcl)	0.25-0.28	0.261
Antennal article III	0.02-0.04	0.032

Antennal article IV	0.04-0.05	0.044
Antennal article V	0.04-0.05	0.044
Left mandible, apical to first marginal (L _A)	0.08-0.09	0.085
Left mandible, first to third marginal (L ₁)	0.14	—
Left mandible, third marginal to molar (L _m)	0.06	—
Right mandible, apical to first marginal (R _A)	0.08-0.09	0.087
Right mandible, first to second marginal (R ₁)	0.10	—
Right mandible, second marginal to molar (R _m)	0.06-0.07	0.064
Mesonotum width (M)	0.19-0.20	0.197
Metanotum width (N)	0.19-0.21	0.196

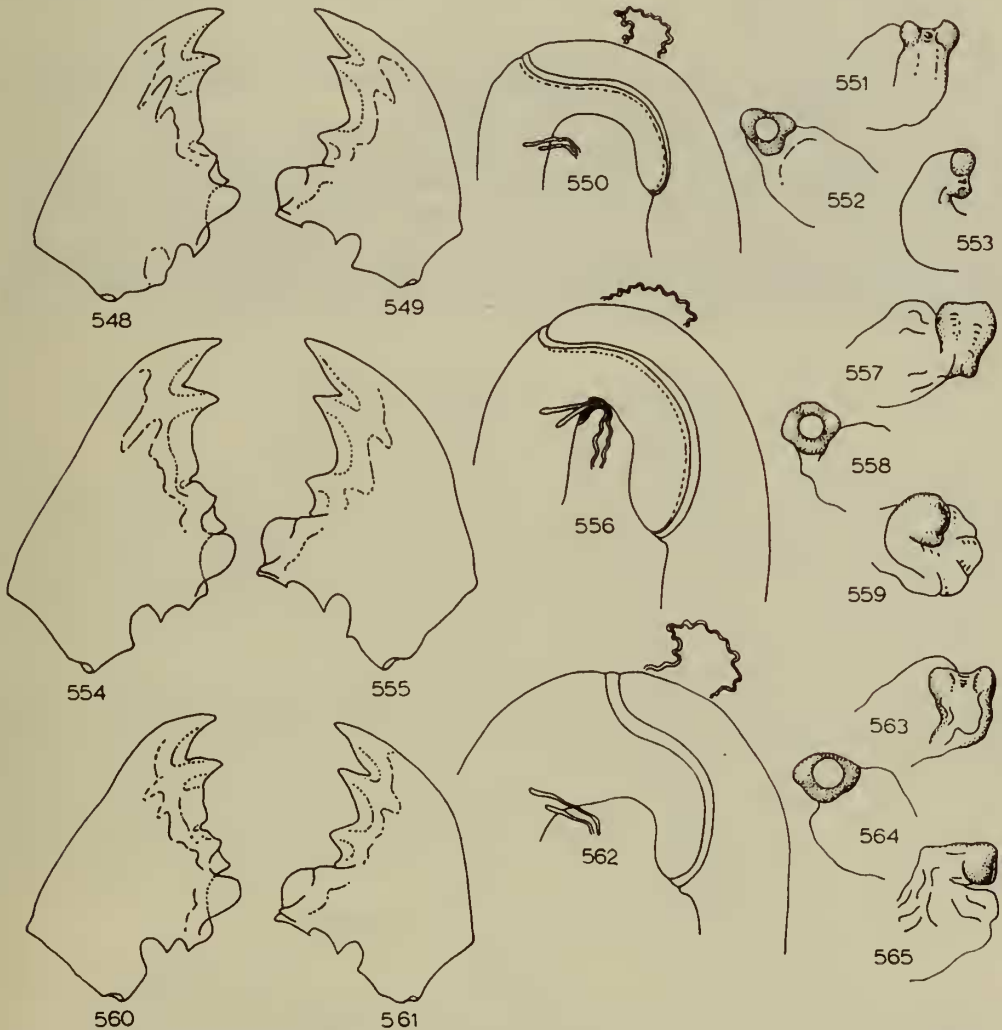
Worker. Head capsule pale yellow, pilosity yellow, fairly dense but short and fine, not conspicuous. Postclypeus strongly inflated, Pcl/W, 0.31-0.34, Pcl/R₁, 2.78-2.86. Apical teeth of mandibles fairly short, L_A/L₁, 0.64-0.66, R_A/R₁, 0.84-0.89; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio, L_A/L₁.L_m, 13.89-14.30; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal shorter than that of second, R_A/R₁.R_m, 18.20-19.20. Fore tibia weakly swollen, T₁/T_w, 4.11-4.23, third apical spur approximately half length of other two. Mesenteric overlap with proctodeum more than four times as long as width of mesenteron at insertion of malpighian tubules, posterior end of mesenteron slightly swollen; enteric valve seating with two weakly developed opposed lobes, connected to second pouch of proctodeum by a short but distinct neck, lateral in unopened abdomen; internal cushions of enteric valve in positions 1 and 2 retracted, very small with scaly surface or at most one or two small spines; position 3 produced through valve opening, tapering distally, armed with 10-12 elongated pectinate spines around the edge, and other prominent spines on the posterior ends of scales on the proximal part of the cushion; position 4 retracted, but about twice as large as positions 1 and 2 and armed with prominent spines on posterior edges of scales; membranous wall of valve between and beyond cushions with sparse minute spicules.

Measurements (two specimens from separate localities) in millimetres.

Head width (W)	0.72-0.73
Fore tibia width (T _w)	0.11
Fore tibia length (T ₁)	0.46-0.48
Postclypeus length (Pcl)	0.22-0.25
Left mandible, apical to first marginal (L _A)	0.07
Left mandible, first to third marginal (L ₁)	0.11
Left mandible, third marginal to molar (L _m)	0.05
Right mandible, apical to first mar- ginal (R _A)	0.07
Right mandible, first to second mar- ginal (R ₁)	0.08-0.09
Right mandible, second marginal to molar (R _m)	0.05

Comparisons between *A. cnaphorus* and *A. amachetus*, *A. ateuchestes* and *A. cicur* have already been made under those species. The imago of *A. disluctans* has rather

shorter mandibular apical teeth, a more prominent postclypeus with evenly rounded posterior margin, and a more distinct fontanelle. *A. hemerus* is much larger, has a less inflated postclypeus and shorter apical teeth. *A. improcinctus* and *A. nanus* are smaller, with the compound eyes markedly flattened against the sides of the head. *A. improelatus* has wider meso- and metanotal constrictions, the posterior margin of the postclypeus is evenly rounded, and the first marginal tooth of the right mandible is longer. *A. polyscolus* is smaller, usually with a large conspicuous oval



FIGS 548-565. *Anenteotermes*, worker mandibles, mesenteric-proctodeal junctions showing attachments of malpighian tubules and positions of malpighian knot, and views of enteric valve seatings. 548-553, *A. disluctans*; 554-559, *A. hemerus*; 560-565, *A. improelatus*.

fontanelle. Its different proportions clearly separated it in principal component analyses shown in Text-fig. 566.

In the worker caste, all species other than the last named are distinguishable from *A. cnaphorus* by their less developed enteric valve armature. The development of cushion position 3 reaches its most specialized form and maximum elongation in *A. polyscolus*. In *A. cnaphorus* it is shorter, slightly wider and tapers more sharply to the tip. This species also has slightly longer mandibular apical teeth, a slightly less swollen fore tibia and is generally a little longer. The abdomen is definitely dehiscent in *A. cnaphorus*.

Holotype ♀ queen, paratype king and workers from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Katanga, Keyberg, near Elizabethville, 23.iv.1948 (*Winifred Emerson*), in American Museum of Natural History.

Other paratype material. DEMOCRATIC REPUBLIC OF CONGO: Katanga, 5 km E. of Elizabethville, 26.iv.1948 (*A. E. Emerson*) in AMNH. MALAWI: 7 m. from Nkata Bay on Ekwendeni Road, 22.ix.1953 (*W. A. Sands & W. Wilkinson*) in BMNH.

The type-colony was found in a small soft mound 4 inches high in 'Dambo', i.e., seasonally flooded grassland. Other records are from the surface layers of a *Macrotermes goliath* mound, and from soil at the foot of an old tree stump.

Anenteotermes disluctans sp. n.

(Text-figs 536-539 & 548-553; Pl. 7, fig. 7)

Imago. Head capsule sepia-brown, darker above ocelli; fontanelle about half as long as ocellus, rather narrow oval, flat or slightly depressed, yellow; medial spot short oval, smaller than fontanelle, flat, coloured as head; postclypeus brown, labrum yellow-brown; frontal marks small slightly depressed brown crescents; antennae yellow-brown. Pronotum brown, meso- and metanota yellow-brown, transverse sutures weak if present; femora pale yellow-brown, tibiae and tarsi yellow. Abdominal tergites yellow-brown, sternites pale yellow-brown laterally, yellow in middle, dorsal and ventral stigmata dark; cerci yellow.

Posterior margin of head capsule evenly rounded; ocelli medium-sized, separated from compound eyes by less than half up to nearly own least diameter, postclypeus moderately to strongly inflated, Pcl/W, 0.28-0.34, posterior margin evenly rounded though not always distinct, median suture present. Apical teeth of mandibles short, L_A/L_1 , 0.46-0.56, R_A/R_1 , 0.62-0.75; subsidiary marginal tooth of left mandible well clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 6.76-8.51, point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edges of marginal teeth equal, complex ratio, $R_1/R_A.R_m$ (note difference from ratio used in worker caste) 22.0-28.5. Pilosity of head capsule brown, dense, uneven, not forming a pelt.

Measurements (nine specimens from five localities) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	0.88-0.96	0.918 \pm 0.028
Ocellus ($O_w \times O_1$)	0.06-0.09 \times 0.09-0.13	0.075 \pm 0.007 \times 0.102 \pm 0.012
Ocellus to eye (O-E)	0.04-0.06	0.044 \pm 0.008
Postclypeus length (Pcl)	0.25-0.31	0.286 \pm 0.010
Antennal article III	0.03-0.05	0.031 \pm 0.007
Antennal article IV	0.04-0.06	0.047 \pm 0.006
Antennal article V	0.04-0.05	0.044 \pm 0.004

Left mandible, apical to first marginal (L_A)	0.08-0.09	0.084 ± 0.005
Left mandible, first to third marginal (L_1)	0.15-0.19	0.166 ± 0.006
Left mandible, third marginal to molar (L_m)	0.06-0.08	0.066 ± 0.004
Right mandible, apical to first marginal (R_A)	0.08-0.09	0.088 ± 0.004
Right mandible, first to second marginal (R_1)	0.11-0.15	0.133 ± 0.004
Right mandible, second marginal (R_m)	0.05-0.06	0.060 ± 0.003
Mesonotum width (M)	0.19-0.23	0.202 ± 0.014
Metanotum width (N)	0.18-0.21	0.198 ± 0.013

Worker. Head capsule and pilosity yellow-white, setae rather numerous but short, fine and pale, inconspicuous. Postclypeus moderately to strongly inflated, $Pc1/W$, 0.27-0.36, $Pc1/R_1$, 1.63-2.50. Apical teeth of mandibles short, L_A/L_1 , 0.46-0.53, R_A/R_1 , 0.54-0.65; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio, $L_A/L_1.L_m$, 9.63-11.85; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal shorter than that of second, $R_A/R_1.R_m$, 11.61-16.65. Fore tibia slightly swollen, T_1/T_w , 4.18-4.41, third apical spur well developed, almost as large as other two. Mesenteric overlap with proctodeum

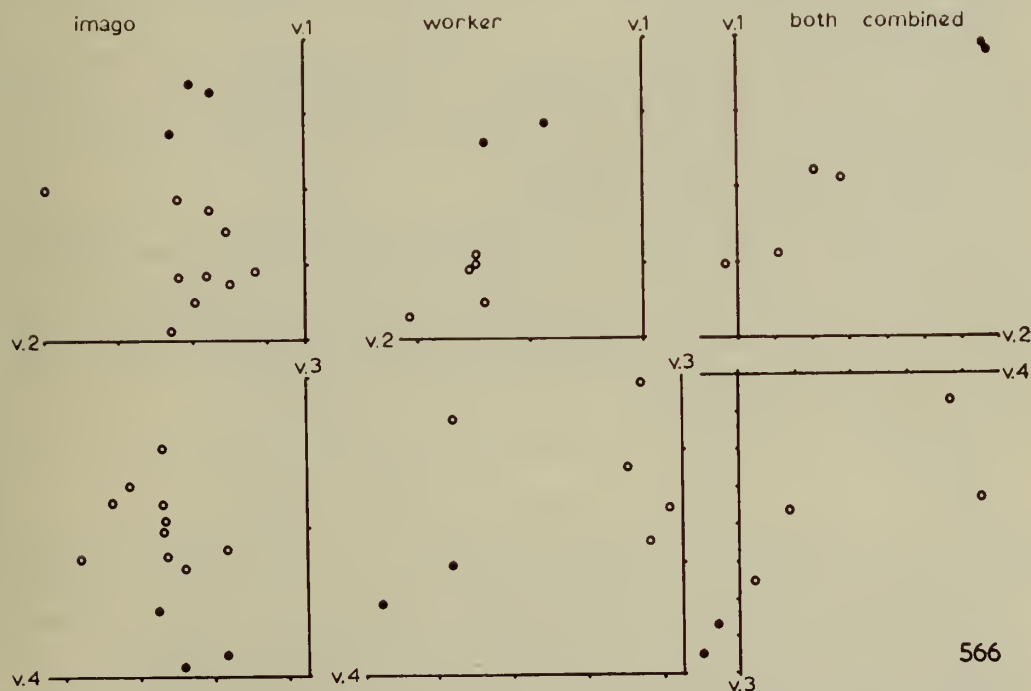


FIG. 566. *Anenteotermes*, distinction between *A. cnaphorus* (spots) and *A. polyscolus* (rings). Plots of principal component scores (transformed variables) corresponding to first, second, third and fourth latent roots of the correlation matrices of the two castes separately and combined.

a little over four times as long as width of mesenteron at insertion of malpighian tubules; enteric valve seating weakly three-lobed, third inner lobe smaller than outer two, connected to second pouch of proctodeum by a short neck, lateral in position in unopened abdomen; internal cushions of enteric valve all retracted with scaly surface only, positions 3 and 4 slightly larger than 1 and 2; membranous wall of valve between and beyond cushions with sparse minute spicules.

Measurements (five specimens from five localities) in millimetres.

	Range	Mean
Head width (W)	0.68-0.75	0.726
Fore tibia width (T _w)	0.11-0.12	0.118
Fore tibia length (T _l)	0.49-0.51	0.506
Postclypeus length (Pcl)	0.19-0.26	0.210
Left mandible, apical to first marginal (L _A)	0.05-0.08	0.069
Left mandible, first to third marginal (L _i)	0.12-0.15	0.136
Left mandible, third marginal to molar (L _m)	0.04-0.05	0.047
Right mandible, apical to first marginal (R _A)	0.06-0.08	0.069
Right mandible, first to second marginal (R _i)	0.09-0.13	0.113
Right mandible, second marginal to molar (R _m)	0.04-0.05	0.043

A. disluctans has already been compared with the species preceding it alphabetically. In the imago caste it is smaller than *A. hemerus*, and has an evenly rounded postclypeus. *A. improcinctus*, *A. nanus* and *A. polyscolus* are smaller than *A. disluctans* and *A. improelatans* has wider meso- and metanotal constrictions, and a vestigial fontanelle.

In the worker caste, *A. hemerus* is again larger, *A. nanus* and *A. polyscolus* have armed enteric valves, and, like *A. improcinctus* are also smaller. The latter species has longer mandibular apical teeth, and the fore tibia is somewhat more swollen. In *A. improelatans* the mixed segment is much shorter and the first marginal tooth of the right mandible is equal to the second.

The material now included in *A. disluctans* was at first separated into two species, one from Uganda and the other from Central Africa. However, it has not been found possible to distinguish the two groups of specimens taxonomically and they are therefore described as one. Some doubt remains because of slight differences in the proportionate sizes of certain parts such as the imago antennal articles. For this reason the central African material is deliberately excluded from the paratype series as a tentative identification.

The abdomen of the worker caste appears to be at least weakly dehiscent in *A. disluctans*.

Holotype ♀ imago, paratype ♂ and ♀ imagos and workers from type-colony, UGANDA: Kawanda, 1948 (*W. V. Harris*, coll. No. 508) in British Museum (Natural History).

Other paratype material. UGANDA: Hoima, 28.viii.1949 (*M. Lüscher*). DEMOCRATIC REPUBLIC OF CONGO: Near Stanleyville (*A. Kohl*), both in AMNH.

Material excluded from type-series. DEMOCRATIC REPUBLIC OF CONGO: Katanga, Keyberg, 10 km S. of Elizabethville, 10.iv.1948 (*A. Emerson*), in AMNH. ZAMBIA: Kitwe (two vials), 25.i.1957 (*W. G. H. Coaton*) in N.C.I., Pretoria.

There is no biological information on this species.

Anenteotermes hemerus sp. n.

(Text-figs 540-543 & 554-559; Pl. 7, fig. 8)

Imago. Head capsule dark sepia-brown, darker above ocelli; fontanelle short oval, about half as large as ocellus, slightly depressed, brown; medial spot oval, flat, smaller than fontanelle, coloured as head; postclypeus sepia-brown, labrum yellow-brown; frontal marks flat crescents, coloured as head; antennal yellow-brown. Pronotum sepia-brown, meso- and metanota yellow-brown, transverse suture only present on mesonotum; femora pale yellow-brown, tibiae and tarsi yellow. Abdominal tergites and dorsal and ventral stigmata brown, sternites pale brown laterally, paler in middle; cerci yellow.

Posterior margin of head capsule evenly rounded; ocelli medium-sized, separated from compound eyes by two-fifths to slightly more than half own least diameter; postclypeus rather weakly inflated, Pcl/W, 0.25, posterior margin bowed, median suture present, weak at each end. Apical teeth of mandibles short, L_A/L_1 , 0.54-0.56, R_A/R_1 , 0.66-0.69; subsidiary marginal tooth of left mandible clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$ 7.37-8.70; points of apical and marginal teeth of right mandible more or less in line, anterior edges of marginal teeth approximately equal or first slightly longer than second, complex ratio, $R_1/R_A.R_m$ (note difference from ratio used in worker caste), 20.60-22.30. Pilosity of head capsule uneven, brown, not forming a pelt.

Measurements (two specimens from one nest-series) in millimetres.

Head width across eyes (W)	0.99-1.06
Ocellus ($O_w \times O_1$)	0.08-0.09 \times 0.11-0.14
Ocellus to eye (O-E)	0.04-0.05
Postclypeus length (Pcl)	0.25-0.26
Antennal article III	0.05
Antennal article IV	0.05-0.06
Antennal article V	0.06
Left mandible, apical to first marginal (L_A)	0.09-0.10
Left mandible, first to third marginal (L_1)	0.17-0.18
Left mandible, third marginal to molar (L_m)	0.07
Right mandible, apical to first marginal (R_A)	0.09
Right mandible, first to second marginal (R_1)	0.13-0.14
Right mandible, second marginal to molar (R_m)	0.07
Mesonotum width (M)	0.22
Metanotum width (N)	0.21

Worker. Head capsule yellow, pilosity orange-yellow, setae numerous but fine and not conspicuous. Postclypeus rather weakly inflated, Pcl/W, 0.26, Pcl/ R_1 , 1.61. Apical teeth of mandibles short, L_A/L_1 , 0.57, R_A/R_1 , 0.64; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 10.31; point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edge of first marginal distinctly shorter than that of second, $R_A/R_1.R_m$, 12.07. Fore tibia slightly swollen, T_1/T_w , 4.50, third apical spur about half as long as other two. Mesenteric overlap with proctodeum about four times as long as width of mesenteron at insertion of malpighian tubules; enteric valve seating very weakly three-lobed, connected to second pouch of proctodeum by a short neck, lateral in position in unopened abdomen; internal cushions of enteric valve all

retracted and about equally developed, with scaly surface only; membranous wall of valve between cushions with very sparse minute spicules.

Measurements (one specimen) in millimetres.

Head width (W)	0.84
Fore tibia width (T_w)	0.13
Fore tibia length (T_l)	0.56
Postclypeus length (Pcl)	0.22
Left mandible, apical to first marginal (L_A)	0.09
Left mandible, first to third marginal (L_1)	0.15
Left mandible, third marginal to molar (L_m)	0.06
Right mandible, apical to first marginal (R_A)	0.09
Right mandible, first to second marginal (R_1)	0.13
Right mandible, second marginal to molar (R_m)	0.05

A. hemerus is the largest species of the genus. Comparisons with *A. amachetus*, *A. ateuchestes*, *A. cicur*, *A. cnaphorus* and *A. disluctans* have already been made. Of the remaining species, *A. improcinctus*, *A. nanus* and *A. polyscolus* are all much smaller and so unlikely to be confused with it. *A. improelatanus* is also smaller, but less markedly so. In the imago it is recognizable by its less constricted meso- and metanota, and very small fontanelle; in the worker caste the first marginal tooth of the right mandible is as long as the second and the mixed segment of the gut is shorter.

The abdomen of the worker appears to be dehiscent in *A. hemerus*.

Holotype ♀ imago, paratype ♂ and ♀ imagos and workers from type-colony, SUDAN: Mount Bangeze, 4°30'N., 30°00'E., 15.v.1937 (*J. G. Myers*) in American Museum of Natural History; paratype ♀ and ♂ imagos and workers from type-colony also in BMNH.

Only the type nest-series is known; there is no biological information. It is known to the Zande tribesmen in the area as 'Akpiaru'.

Anenteotermes improcinctus sp. n.

(Text-figs 567-570 & 583-588)

Imago. Head capsule sepia-brown, darker above ocelli; fontanelle very small elongate oval, flat or slightly depressed, brown, almost obsolete in some specimens; medial spot also very small, elongate oval, flat, coloured as head; postclypeus brown, labrum pale yellow-brown; frontal marks smooth, flat, semicircular, coloured as head; antennae pale brown to brown. Pronotum, meso- and metanota, brown, transverse sutures present; femora and tibiae pale brown, tarsi pale yellow. Abdominal tergites and dorsal stigmata brown, sternites pale brown, paler in middle, ventral stigmata pale; cerci pale yellow-brown.

Posterior margin of head capsule evenly rounded; ocelli rather small, separated from somewhat flattened compound eyes by one-quarter to slightly over one-third own least diameter; postclypeus rather strongly inflated, Pcl/W, 0.30-0.34, posterior margin evenly rounded, median suture only distinct in middle. Apical teeth of mandibles short, L_A/L_1 , 0.50-0.60, R_A/R_1 ,

0.67-0.86; subsidiary marginal tooth of left mandible only just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 11.42-12.91; point of first marginal tooth of right mandible only slightly behind line of apical to second marginal, anterior edges of marginal teeth approximately equal in length, complex ratio, $R_1/R_A.R_m$ (note difference from ratio used in worker caste), 26.00-30.00. Pilosity of head capsule uneven, yellow, not forming a pelt.

Measurements (four specimens from two localities) in millimetres

	Range	Mean
Head width across eyes (W)	0.69-0.71	0.703
Ocellus ($O_w \times O_l$)	0.07-0.08 \times 0.09	0.070 \times 0.088
Ocellus to eye (O-E)	0.02-0.03	0.021
Postclypeus length (Pcl)	0.21-0.24	0.228
Antennal article III	0.02-0.03	0.022
Antennal article IV	0.03-0.04	0.033
Antennal article V	0.03	0.029
Left mandible, apical to first marginal (L_A)	0.06-0.07	0.066
Left mandible, first to third marginal (L_1)	0.12-0.13	0.120
Left mandible, third marginal to molar (L_m)	0.04-0.05	0.046
Right mandible, apical to first marginal (R_A)	0.06-0.08	0.069
Right mandible, first to second marginal (R_1)	0.09-0.10	0.091
Right mandible, second marginal to molar (R_m)	0.05	0.048
Mesonotum width (M)	0.16-0.17	0.159
Metanotum width (N)	0.15-0.16	0.155

Worker. Head capsule yellow-white, pilosity sparse, fine, yellow. Postclypeus rather strongly inflated, Pcl/W , 0.35-0.36, Pcl/R_1 , 2.66-3.00. Apical teeth of mandibles short, L_A/L_1 , 0.61-0.63, R_A/R_1 , 0.77-0.78; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 17.87-18.52; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal shorter than that of second, $R_A/R_1.R_m$, 20.90-21.10. Fore tibia moderately swollen, T_1/T_w , 3.85-4.00, third apical spur short, about one-third length of other two. Mesenteric overlap with proctodeum about four times as long as width of mesenteron at insertion of malpighian tubules, or a little less; enteric valve seating scarcely lobed, almost a rim, sessile on second pouch of proctodeum, dorso-lateral in position in unopened abdomen; internal cushions of enteric valve all retracted, about equally developed, with scaly surface only; membranous wall of valve between and beyond cushions with very sparse minute spicules.

Measurements (two specimens from different localities) in millimetres.

Head width (W)	0.60-0.63
Fore tibia width (T_w)	0.10
Fore tibia length (T_1)	0.38-0.40
Postclypeus length (Pcl)	0.21-0.23
Left mandible, apical to first marginal (L_A)	0.06
Left mandible, first to third marginal (L_1)	0.10
Left mandible, third marginal to molar (L_m)	0.03

Right mandible, apical to first marginal (R_A)	0.06
Right mandible, first to second marginal (R_1)	0.08
Right mandible, second marginal to molar (R_m)	0.04

A. improcinctus is one of the three smallest species of the genus, only *A. nanus* being smaller, and this species has the first marginal tooth of the right mandible shorter than the second in the imago, longer apical teeth in both castes, and an armed enteric valve in the worker. *A. polyscolus* is about the same size, but in the imago the fontanelle is larger and more conspicuous and the pilosity forms a pelt; the apical teeth are longer in both castes and the characteristic enteric valve is easily recognized. The remaining species, *A. improelatanus*, is larger and has less constricted meso- and metanota in the imago; the worker has a shorter mixed segment. The abdomen of the worker caste appears to be dehiscent in *A. improcinctus*.

Holotype ♀ imago, paratype ♂ and ♀ imagos, and workers from type-colony, NIGERIA: Northern Region, 20 miles from Yandev (near Gboko) on Makurdi Road, 25.ii.1958 (*W. A. Sands* Coll., No. S.1928), in British Museum (Natural History).

Other paratype material. NIGERIA: Eastern Region, Nsukka, 20 miles from Enugu on Oturkpo Road, 5.iii.1958 (*W. A. Sands* No. S.2040); Northern Region, Beli, 20 m. S.E. of Bakundi on Taraba River, 19.v.1957 (*W. A. Sands*) also in BMNH. IVORY COAST: Séguéla, 24.vi.1964 (*E. Ernst*) in Swiss Tropical Institute, Basle.

Anenteotermes improelatanus sp. n.

(Text-figs 544-547 & 550-565)

Imago. Head capsule dark chestnut-brown, not appreciably darker above ocelli; fontanelle vestigial, flat, minute oval spot, slightly paler than head; medial spot circular, flat, slightly larger than fontanelle, coloured as head; postclypeus brown, labrum yellow-brown; frontal marks semicircular, distinct, flat, brown; antennae pale brown. Pronotum, meso- and metanota, sepia-brown, transverse sutures weak or absent; femora brown, tibiae yellow-brown tarsi yellow. Abdominal tergites brown, dorsal stigmata sepia-brown, sternites pale brown yellow-brown in middle, ventral stigmata brown; cerci yellow.

Posterior margin of head capsule slightly undulating, not quite evenly rounded; ocelli medium-sized, separated from compound eyes by up to half own least diameter; postclypeus moderately inflated, Pcl/W , 0.27-0.31, posterior margin more or less evenly rounded, median suture distinct. Apical teeth of mandibles short, L_A/L_1 , 0.54-0.59, R_A/R_1 , 0.74-0.82; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio, $L_A/L_1.L_m$, 8.75-9.89; points of apical and marginal teeth of right mandible in line, anterior edge of first marginal distinctly longer than that of second, complex ratio, $R_1/R_A.R_m$ (note difference from ratio used in worker caste), 19.5-26.5. Pilosity of head capsule relatively even, forming a pelt, but with some uneven emergent setae, brown. Meso- and metanota wider at constrictions, M/W , 0.28-0.31.

Measurements (six specimens from three nest series) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	0.85-0.94	0.890 \pm 0.041
Ocellus ($O_w \times O_l$)	0.07-0.08 \times 0.09-0.10	0.074 \pm 0.005 \times 0.096 \pm 0.007
Ocellus to eye ($O-E$)	0.02-0.04	0.029 \pm 0.007

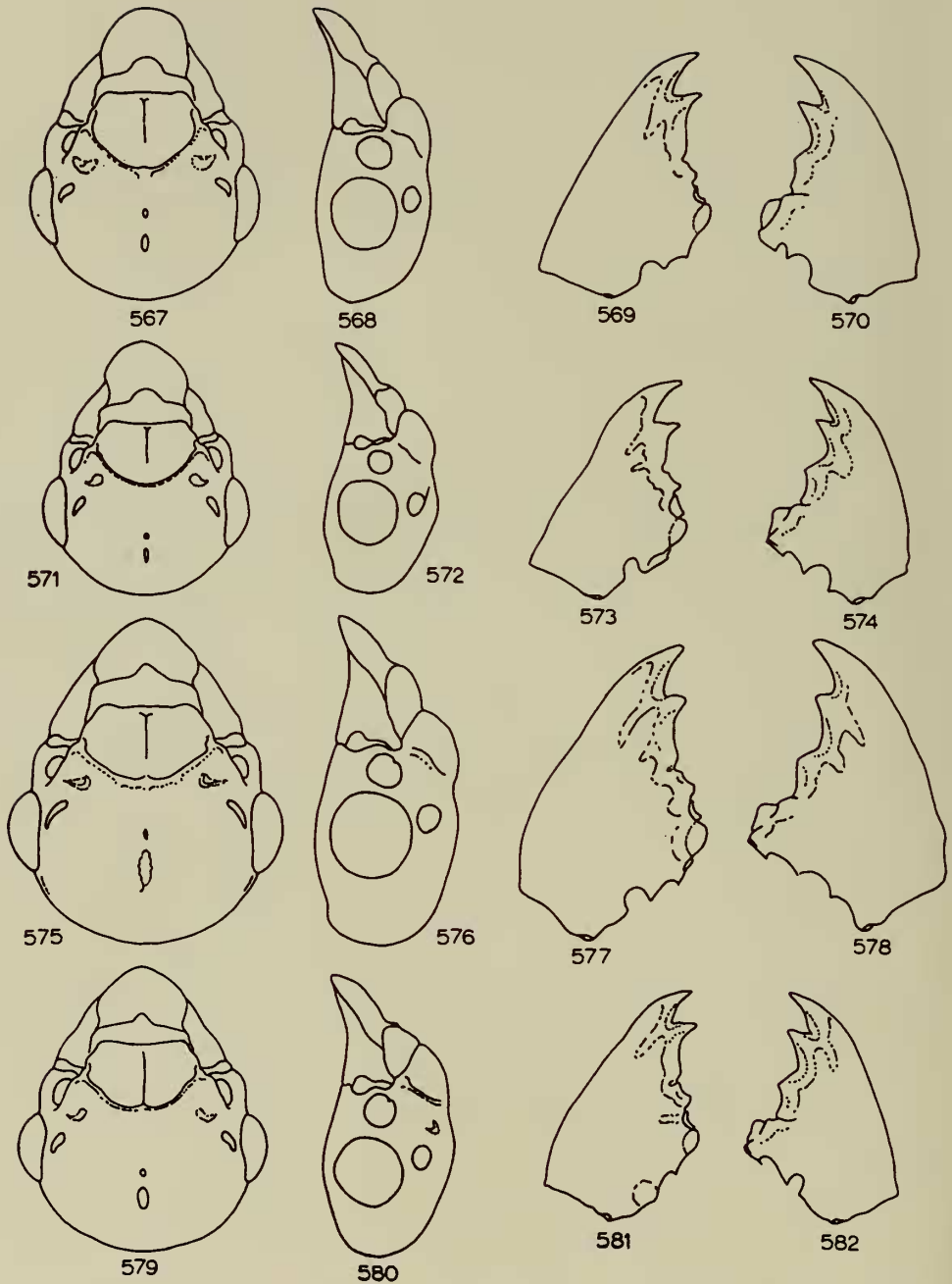
Postclypeus length (Pcl)	0.25-0.29	0.264 ± 0.106
Antennal article III	0.02-0.24	0.029 ± 0.006
Antennal article IV	0.04-0.05	0.041 ± 0.005
Antennal article V	0.04-0.05	0.040 ± 0.004
Left mandible, apical to first marginal (L _A)	0.07-0.08	0.075 ± 0.004
Left mandible, first to third marginal (L ₁)	0.12-0.14	0.133 ± 0.007
Left mandible, third marginal to molar (L _m)	0.06	0.061 ± 0.001
Right mandible, apical to first marginal (R _A)	0.08-0.09	0.080 ± 0.004
Right mandible, first to second marginal (R ₁)	0.09-0.11	0.102 ± 0.004
Right mandible, second marginal to molar (R _m)	0.05-0.06	0.057 ± 0.005
Mesonotum width (M)	0.24-0.28	0.260 ± 0.020
Metanotum width (N)	0.24-0.29	0.270 ± 0.020

Worker. Head capsule pale yellow, pilosity yellow, setae sparse. Postclypeus rather strongly inflated, Pcl/W, 0.31-0.34. Pcl/R₁, 2.47-2.67. Apical teeth of mandibles short, L_A/L₁, 0.59-0.64, R_A/R₁, 0.78-0.82; subsidiary marginal tooth of left mandible separated from molar plate by distinct notch in surface view, complex ratio, L_A/L₁.L_m, 12.20-13.49; point of first marginal tooth of right mandible slightly behind line of apical to second marginal, anterior edges of marginal teeth equal in length, R_A/R₁.R_m, 15.12-18.60. Fore tibia scarcely swollen, T₁/T_w, 4.51-4.73, third apical spur about one-third length of other two, pale and inconspicuous. Mesenteric overlap with proctodeum rather short, less than three times as long as width of mesenteron at insertion of malpighian tubules; enteric valve seating with two very weakly developed opposed lobes and a very small third inner lobe, connected to second pouch of proctodeum by a short neck; lateral in position in unopened abdomen; internal cushions of enteric valve all retracted, about equally developed, with scaly surface only; membranous wall of valve between and beyond cushions with sparse minute spicules.

Measurements (three specimens from separate nest series) in millimetres.

	Range	Mean
Head width (W)	0.74-0.78	0.761
Fore tibia width (T _w)	0.11-0.12	—
Fore tibia length (T ₁)	0.51-0.54	0.525
Postclypeus length (Pcl)	0.24-0.25	0.244
Left mandible, apical to first marginal (L _A)	0.07-0.08	0.075
Left mandible, first to third marginal (L ₁)	0.12-0.13	0.123
Left mandible, third marginal to molar (L _m)	0.04-0.05	0.048
Right mandible, apical to first marginal (R _A)	0.07-0.08	0.076
Right mandible, first to second marginal (R ₁)	0.09-0.10	0.095
Right mandible, second marginal to molar (R _m)	0.04-0.05	0.048

A. improlatans has already been compared with all those preceding it alphabetically. It is easily recognized by its rather wider meso- and metanotal constrictions in the imago and its shorter mixed segment in the worker, quite apart from the different proportions of the mandibles in both castes. The remaining two species of the genus, *A. nanus* and *A. polyscolus*, are both smaller, with rather flattened compound eyes in the imago. In the worker caste, both have spiny armature in the enteric valve.



FIGS 567-582. *Anenteotermes*, imago head capsule, front and side views, and imago mandibles. 567-570, *A. improcinctus*; 571-574, *A. nanus*; 575-578, *A. cnaphorus*; 579-582, *A. polyscolus*.

Holotype ♀ imago, paratype ♂ and ♀ imagos, and workers from type-colony, KENYA: 9 m. from Londiani on Kisumu Road, alt. over 7,000 ft, 19.ii.1964 (*R. M. C. Williams* Coll. No. RW9) in British Museum (Natural History).

Other paratype material. KENYA: Kaptagat, 3.iv.1952 (*W. V. Harris*); same data (*W. A. Sands*) also in BMNH.

The species has been recorded from the mounds of *Cubitermes* and *Odontotermes* only at high altitudes in montane grassland.

Anenteotermes nanus (Sjöstedt) **comb. n.**

(Text-figs 571–574 & 589–594; Pl. 8, fig. 2)

Eutermes nanus Sjöstedt, 1911: 161. LECTOTYPE ♀, DEMOCRATIC REPUBLIC OF CONGO: Mukimbungu (Naturhistoriska Riksmuseum, Stockholm) here designated [examined].

Imago. Head capsule (colours probably somewhat faded) brown, not appreciably darker above ocelli; fontanelle very small oval, flat, slightly paler than head; medial spot oval, about equal in size to fontanelle, slightly raised on small bump, coloured as head; postclypeus a little paler than head, labrum yellow, frontal marks flat crescents, coloured as head; antennae pale yellow-brown. Pronotum, meso- and metanota pale brown, transverse sutures present; femora and tibiae yellow, tarsi pale yellow. Abdominal tergites pale brown, dorsal stigmata paler, sternites and ventral stigmata very pale brown; cerci yellow.

Posterior margin of head capsule more or less evenly rounded; ocelli medium-sized, separated from compound eyes by slightly more than half up to nearly own least diameter; postclypeus moderately inflated, Pcl/W, 0.29–0.32, posterior margin evenly rounded, median suture present, weak in some specimens. Apical teeth of mandibles moderately long, L_A/L_1 , 0.67–0.76, R_A/R_1 , 0.84–1.00; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 13.20–15.92; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal shorter than that of second, complex ratio, $R_1/R_A.R_m$ (note difference from ratio used in worker caste), 21.1–23.9. Pilosity of head capsule fairly even, forming a slightly rough pelt with emergent setae, brown.

Measurements (three specimens from two localities) in millimetres.

	Range	Mean
Head width across eyes (W)	0.65–0.69	0.670
Ocellus ($O_w \times O_1$)	0.05–0.06 × 0.08–0.09	0.055 × 0.085
Ocellus to eye (O–E)	0.03–0.05	0.040
Postclypeus length (Pcl)	0.19–0.21	0.202
Antennal article III	0.02	—
Antennal article IV	0.02–0.03	0.024
Antennal article V	0.02–0.04	0.028
Left mandible, apical to first marginal (L_A)	0.06–0.07	0.066
Left mandible, first to third marginal (L_1)	0.09–0.10	0.092
Left mandible, third marginal to molar (L_m)	0.05	—
Right mandible, apical to first marginal (R_A)	0.07	0.066
Right mandible, first to second marginal (R_1)	0.07–0.08	0.074

Right mandible, second marginal to molar (R _m)	0.05	—
Mesonotum width (M)	0.14-0.16	0.146
Metanotum width (N)	0.15-0.16	0.157

Worker. Head capsule and pilosity pale yellow, setae sparse. Postclypeus moderately inflated, Pcl/W, 0.27-0.31, Pcl/R₁, 2.20-2.75. Apical teeth of mandibles fairly long, L_A/L₁, 0.69-0.73, R_A/R₁, 0.82-0.88; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio, L_A/L₁.L_m, 14.81-16.20; point of first marginal tooth of right mandible, distinctly behind line of apical to second marginal, anterior edge of first marginal much shorter than that of second, R_A/R₁.R_m, 20.50-20.70. Fore tibia moderately swollen, T₁/T_w, 3.61-3.78, third apical spur about half length of other two. Mesenteric overlap with proctodeum rather more than four times as long as width of mesenteron at insertion of malpighian tubules; enteric valve seating sessile on second pouch of proctodeum, without a neck, very weakly two-lobed, dorsolateral in position in unopened abdomen; internal cushions of enteric valve all more or less equally developed, protruding slightly through valve opening, surface scaly, scales in posterior one-third of length of cushion developed into small to pronounced spines; membranous wall of valve between and beyond cushions with rather numerous minute spicules.

Measurements (two specimens from separate localities) in millimetres.

Head width (W)	0.56
Fore tibia width (T _w)	0.10
Fore tibia length (T ₁)	0.38
Postclypeus length (Pcl)	0.15-0.18
Left mandible, apical to first marginal (L _A)	0.06
Left mandible, first to third marginal (L ₁)	0.08
Left mandible, third marginal to molar (L _m)	0.05
Right mandible, apical to first marginal (R _A)	0.06
Right mandible, first to second marginal (R ₁)	0.06-0.07
Right mandible, second marginal to molar (R _m)	0.04

The smallest species of the genus, *A. nanus* has already been compared with all the remaining members other than *A. polyscolus*. The latter species has longer apical mandibular teeth in both castes, a more conspicuous fontanelle in the imago and in the worker, the fully developed enteric valve armature with cushion position 3 elongated and armed with long pectinate spines. The abdomen of the worker caste appears to be dehiscent in *A. nanus*.

A lectotype is designated below from among the existing syntype material of *A. nanus* (Sjöstedt).

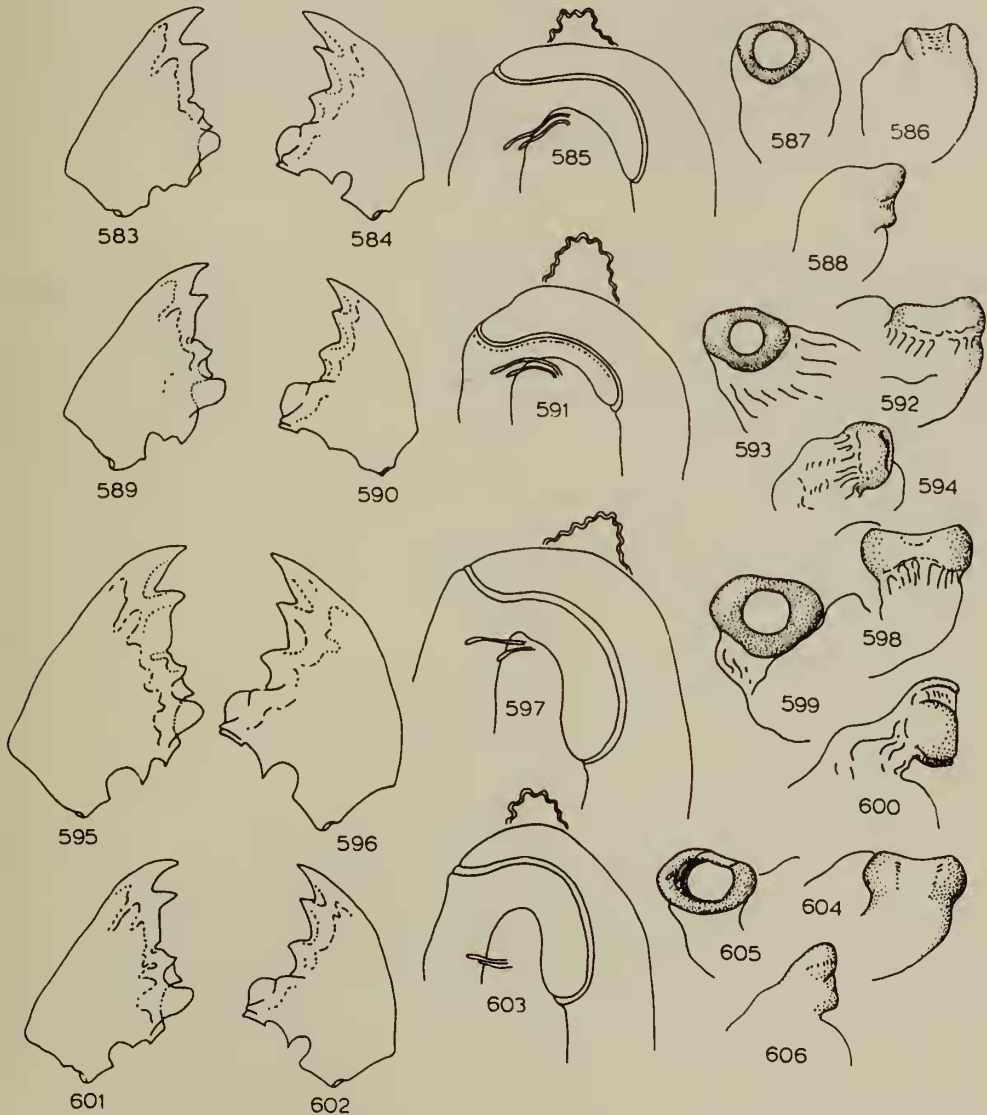
Type-material. *Eutermes nanus* Sjöstedt, LECTOTYPE ♀ imago, paralectotype ♂ and ♀ imagos, and workers from type-colony, DEMOCRATIC REPUBLIC OF CONGO: Mukumungu, ix.1904 (*K. E. Laman*), in Naturhistoriska Riksmuseum, Stockholm; other paralectotypes in AMNH.

Other material. DEMOCRATIC REPUBLIC OF CONGO: Camp Putnam, Epulu River, 17.v.1948 (*A. E. Emerson*) in AMNH.

Anenteotermes polyscolus sp. n.

(Text-figs 566, 579-582 & 601-606; Pl. 8, figs 4-6)

Imago. Head capsule sepia-brown, darker above ocelli; fontanelle oval to elongate oval, slightly smaller than ocellus, slightly depressed, yellow; medial spot oval, flat, smaller than fontanelle, coloured as head; postclypeus brown, labrum yellow-brown; frontal marks flat



FIGS 583-606. *Anenteotermes*, worker mandibles, mesenteric-proctodeal junctions showing attachments of malpighian tubules and positions of malpighian knot, and views of enteric valve seatings. 583-588, *A. improcinctus*; 589-594, *A. nanus*; 595-600, *A. cnaphorus*; 601-606, *A. polyscolus*.

brown crescents; antennae yellow. Pronotum brown, meso- and metanota yellow-brown, transverse sutures present, weak in some specimens; femora and tibiae yellow, tarsi paler. Abdominal tergites brown, dorsal stigmata sometimes slightly darker, lateral parts of sternites and ventral stigmata brown, sternites yellow in middle; cerci pale yellow.

Posterior margin of head capsule evenly rounded; ocelli rather small, separated from compound eyes by one-third, up to four-fifths own least diameter; postclypeus weakly to moderately inflated, Pcl/W , 0.23-0.31, posterior margin arched or slightly bowed, not evenly rounded, median suture usually distinct. Apical teeth of mandibles short, L_A/L_1 , 0.42-0.57, R_A/R_1 , 0.63-0.74; subsidiary marginal tooth of left mandible just clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 8.00-9.30; apical and marginal teeth of right mandible approximately in line, anterior edges of first and second marginal teeth equal in length, complex ratio, $R_1/R_A.R_m$ (note difference from ratio used in worker caste), 21.7-29.9. Pilosity of head capsule pale yellow, a short fine pelt with emergent setae in most specimens, less even in some.

Measurements (10 specimens from six localities) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	0.69-0.79	0.745 \pm 0.030
Ocellus ($O_w \times O_l$)	0.06-0.08 \times 0.08-0.10	0.066 \pm 0.007 \times 0.087 \pm 0.009
Ocellus to eye (O-E)	0.02-0.05	0.041 \pm 0.008
Postclypeus length (Pcl)	0.17-0.24	0.196 \pm 0.025
Antennal article III	0.01-0.03	0.021 \pm 0.006
Antennal article IV	0.03-0.05	0.036 \pm 0.006
Antennal article V	0.03-0.04	0.036 \pm 0.006
Left mandible, apical to first marginal (L_A)	0.05-0.07	0.060 \pm 0.007
Left mandible, first to third marginal (L_1)	0.10-0.13	0.124 \pm 0.005
Left mandible, third marginal to molar (L_m)	0.05-0.06	0.055 \pm 0.006
Right mandible, apical to first marginal (R_A)	0.06-0.07	0.063 \pm 0.005
Right mandible, first to second marginal (R_1)	0.09-0.10	0.092 \pm 0.005
Right mandible, second marginal to molar (R_m)	0.05-0.06	0.056 \pm 0.004
Mesonotum width (M)	0.16-0.20	0.173 \pm 0.011
Metanotum width (N)	0.16-0.20	0.175 \pm 0.014

Worker. Head capsule pale yellow, pilosity sparse, yellow. Postclypeus moderately to strongly inflated, Pcl/W , 0.28-0.35, Pcl/R_1 , 2.30-3.02. Apical teeth of mandibles short, L_A/L_1 , 0.50-0.60, R_A/R_1 , 0.68-0.80; subsidiary marginal tooth of left mandible separated from molar prominence by distinct notch in surface view, complex ratio, $L_A/L_1.L_m$, 12.52-14.60; point of first marginal tooth of right mandible distinctly behind line of apical to second marginal, anterior edge of first marginal distinctly shorter than that of second, $R_A/R_1.R_m$, 16.60-18.30. Fore tibia moderately swollen, T_1/T_w , 3.58-4.05, third apical spur small, but not vestigial, about one-quarter length of other two. Mesenteric overlap with proctodeum from four to five and a half times as long as width of mesenteron at insertion of malpighian tubules; enteric valve seating very weakly two-lobed, connected to second pouch of proctodeum by a very short neck, lateral in position in unopened abdomen; internal cushions of enteric valve in positions 1 and 2 retracted, very small, with scaly surface on at most one or two small spines; position 3 produced through valve opening, cylindrical, tapering distally and armed with 10-15 elongated pectinate spines around the edge, and other prominent spines on the posterior ends of scales on the proximal part of the cushion; position 4 retracted, similar in size to position 2,

with scaly surface and one or two small spines; membranous wall of valve between and beyond cushions with sparse minute spicules.

Measurements (five specimens from separate localities) in millimetres.

	Range	Mean \pm S.D.
Head width (W)	0.60-0.64	0.621 \pm 0.081
Fore tibia width (T _w)	0.11-0.12	0.111 \pm 0.006
Fore tibia length (T _l)	0.43-0.45	0.433 \pm 0.011
Postclypeus length (Pcl)	0.17-0.22	0.186 \pm 0.020
Left mandible, apical to first marginal (L _A)	0.05-0.06	0.053 \pm 0.005
Left mandible, first to third marginal (L _i)	0.10	—
Left mandible, third marginal to molar (L _m)	0.04	—
Right mandible, apical to first marginal (R _A)	0.05-0.06	0.054 \pm 0.003
Right mandible, first to second marginal (R _i)	0.07-0.08	0.054 \pm 0.003
Right mandible, second marginal to molar (R _m)	0.04	—

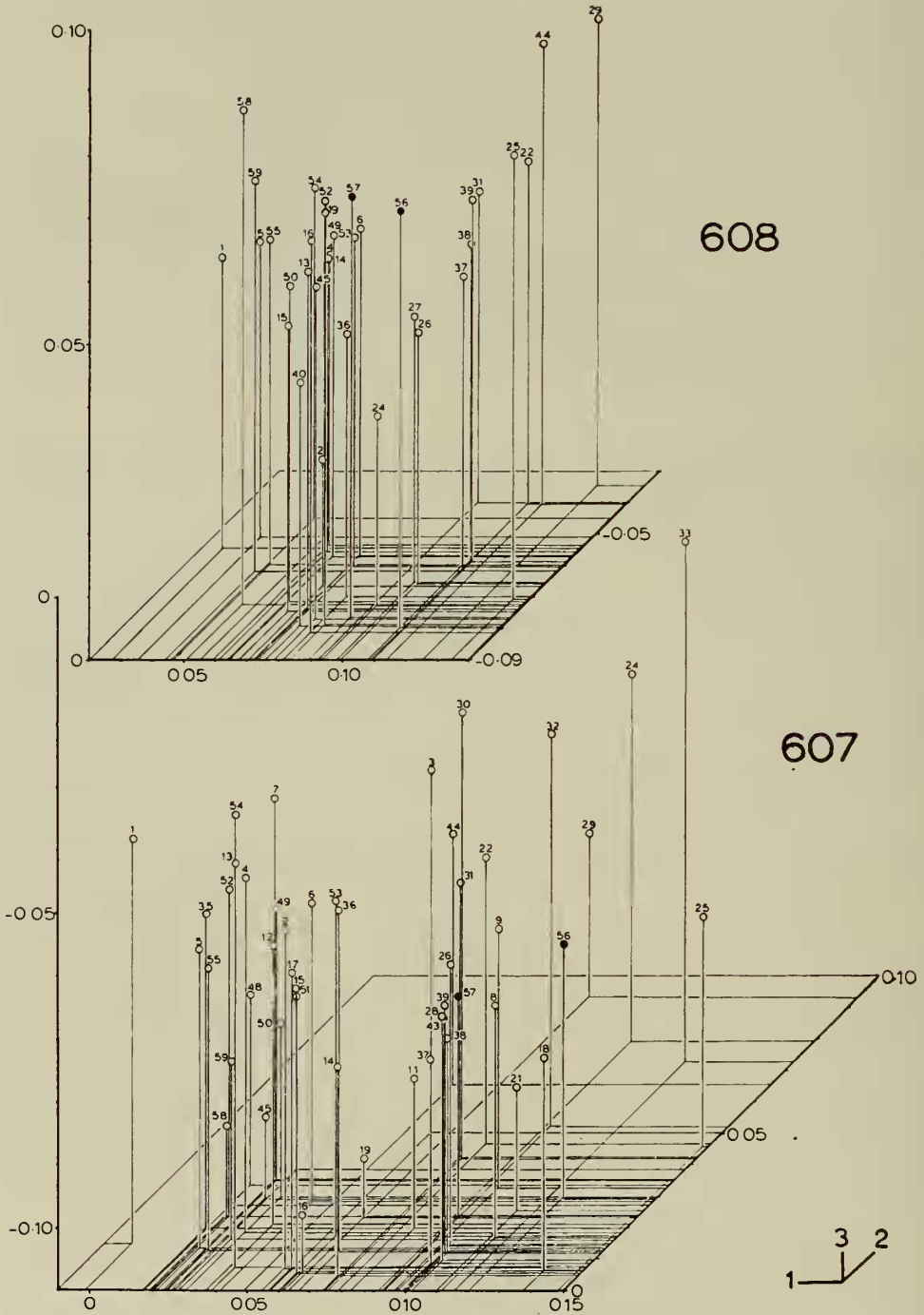
A. polyscolus has already been compared with the other members of the genus under their own descriptions. The abdomen of the worker caste is probably dehiscent, though few specimens show clear signs of this in the preserved material.

There is a fair amount of variation in the enteric valve armature, the imago head pilosity and fontanelle, and even in the proportions of the mandibular teeth, among the specimens included in this species. It may well be that when more material is found it will be necessary to divide it into an eastern and a western species. However, the differences observed in the existing specimens are not clear enough to justify separation at present. One or two specimens are outliers in some dimensions of the principal component analysis (Text-fig. 566) almost as distant from the main clump as those of *A. cnaphorus*. This is largely a reflection of the mandible variation mentioned above.

Holotype ♀ imago, paratype ♂ and ♀ imagos and workers from type-colony, GHANA: 10 m. N. of Wenchi on Bamboi Road, 30.iii.1959 (*W. A. Sands* Coll., No. S.2689), in British Museum (Natural History).

Other paratype material. GHANA: 5½ m. from Dunkwa on Obuasi Road, 4.iv.1959 (*W. A. Sands*); Aburi, 1926 (*W. H. Patterson*). IVORY COAST: Youhouli, 10 km N. of Dabou, 13.v.1963 and 'Basse Cote D'Ivoire' (*P. Bodot*). SIERRA LEONE: Freetown, 8.i.1958 (*W. Wilkinson*). GUINEA: Mount Nimba, Route de Keoulenta, x.1951 (*M. Lamotte*) in AMNH. NIGERIA: Northern Region, Fan, near Forum, Jos plateau, 25.vii.1957, 3 m. from Ankpa on Dekina Road, 6.iii.1958; Western Region, 27 m. S. of Ilorin on Oyo Road, 4.xii.1957 and between Shagamu and Ijebu-Ode, 14.xii.1957 (*W. A. Sands*); Eastern Region, 40 m. from Port Harcourt on Owerri Road, 19.iii.1957 (*W. Wilkinson*). CAMEROUN: Mamfe, 27.v.1957 (*W. Wilkinson*). DEMOCRATIC REPUBLIC OF CONGO: Stanleyville, 26.v.1948 (*A. Emerson*), in AMNH.

All material is in the British Museum (Natural History) unless otherwise stated. Fourteen nest-series have been examined. Most of the records are from the mounds of other species, either *Cubitermes*, *Proculitermes* or *Macrotermes*. Some are from loose soil near tree roots and the habitats range from dense rain forest to Northern Guinean Savanna.



FIGS 607 & 608. Three dimensional graphs of canonical variates 1, 2 & 3 showing species of *Aderitotermes* as solid spots. 607, imago; 608, worker caste.

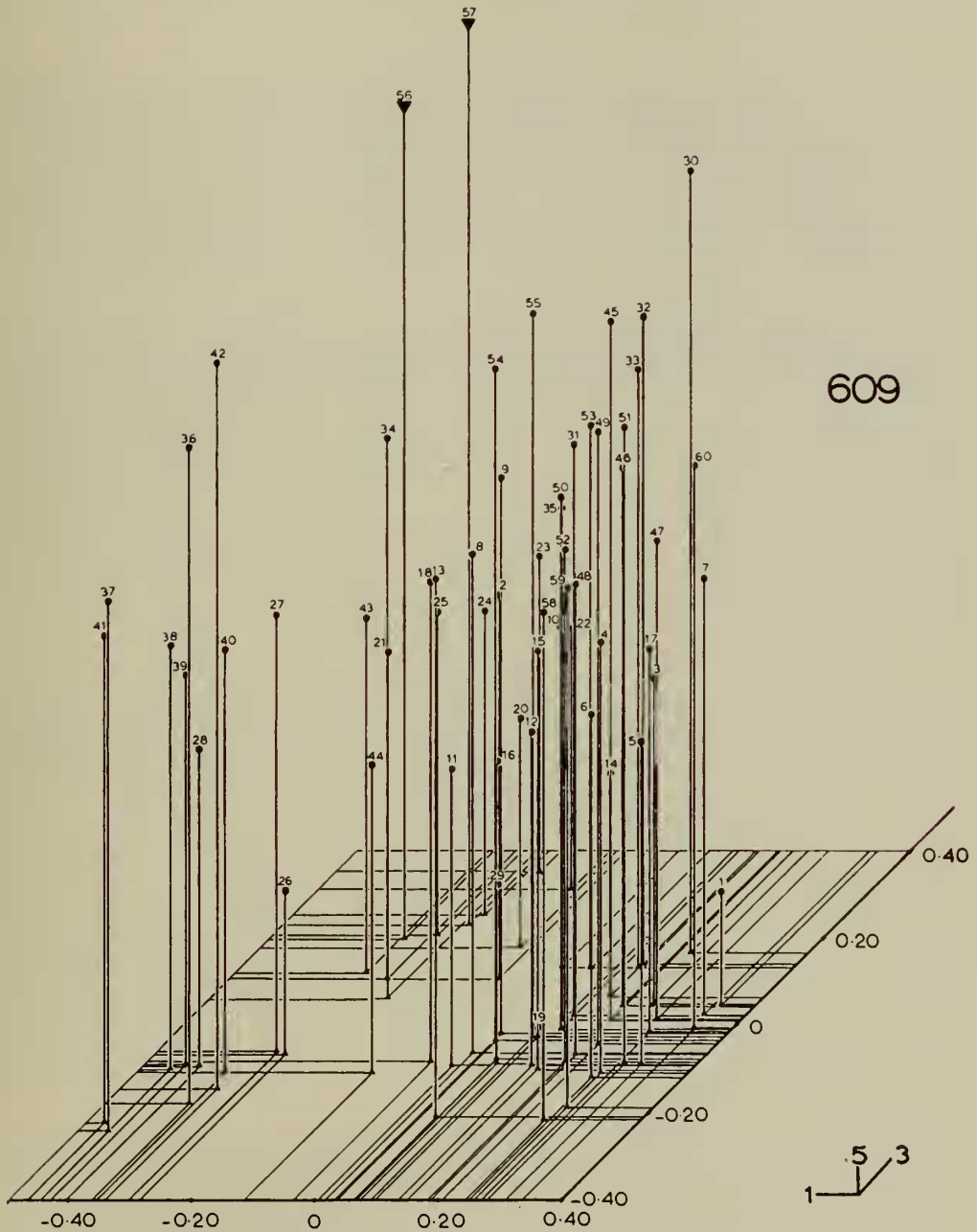


FIG. 609. Three-dimensional graph of principal co-ordinates analysis-plots of eigenvectors 1, 3 & 5 showing species of *Aderitotermes* marked by large triangles.

ADERITOTERMES gen. n.

(Aderitos, Gr., 'without strife')

Type-species: *Aderitotermes fossor* sp. n.

Imago. Large, W, 1.04–1.31. Fore tibia with three apical spurs, third well developed, about two-thirds length of other two. Apical teeth of mandibles fairly short, L_A/L_1 , 0.54–0.68, R_A/R_1 , 0.73–1.06; subsidiary marginal tooth of left mandibles separated from molar prominence by a distinct notch in surface view, $L_A/L_1.L_m$. Right mandible with points of apical and marginal teeth approximately in line, anterior edges of first and second marginals equal in length. Fontanelle circular to short oval, distinct, conspicuously paler than head capsule. Pilosity of head a short, fine, even silvery pelt, with emergent setae. Meso- and metanota fairly wide at constrictions, M/W , 0.28–0.34, transverse dark sutures present; complex ratio of mandible and notal measurements, $L_1/M.N$, 1.26–2.05.

Worker. Large, W, 0.90–0.99. Fore tibia weakly to scarcely swollen, T_1/T_w , 4.21–5.31, with three apical spurs, third about half length of other two. Apical teeth of mandibles fairly short to moderately long, L_A/L_1 , 0.60–0.79, R_A/R_1 , 0.78–1.00; subsidiary marginal tooth of left mandible separated from molar prominence by a distinct notch in surface view, complex ratio, $L_A/L_1.L_m$, 11.69–14.10. Right mandible with point of first marginal tooth slightly behind line of apical to second marginal, anterior edges of marginal teeth equal in length, complex ratio, $R_A/R_1.R_m$, 13.80–17.45. Mesenteric junction with proctodeum overlapping, elongated to form a distinct mixed segment, four to five times as long as width of mesenteron at insertion of malpighian tubules, proximal end of proctodeum well to left of malpighian knot. Enteric valve seating with three prominent equal lobes, regularly spaced, connected to second pouch of proctodeum by distinct to very elongated neck, fully dorsal in position in unopened abdomen; internal cushions of enteric valve retracted, or produced distally through valve opening, not sclerotized, scales on cushion surfaces, and membranous wall of valve between and beyond cushions fringed with minute to prominent spicules.

This genus is fairly readily recognized in the imago by the conspicuous fontanelle, combined with the very short, fine, even silvery pilosity of the head capsule and the large size. The only sympatric species with superficial similarity is *Astratotermes prosenus*, and this is larger with uneven pilosity. In the worker caste, the elongated mixed segment distinguishes *Aderitotermes* from most other genera. Of the two genera with this feature similarly developed, *Adaiphrotermes* has a swollen end to the mesenteron, and only two apical spurs on the fore tibia. *Anenteotermes* is smaller, and the enteric valve seating and armature is different.

Aderitotermes is one of the more isolated genera in the analyses of the similarity matrix. In both single linkage clustering and median sorting it lies adjacent to *Amicotermes*, which is reflected on the first five of the principal co-ordinates other than the second (Text-fig. 609). The similarity of the enteric valve armature between those genera may result from a genuine relationship. *Amicotermes* has no mixed segment and longer mandibular apical teeth, being more primitive in the former and more specialized in the latter character.

The two species of *Aderitotermes* described here resemble each other very closely in every feature except the enteric valve armature. The latter character is so widely different as to appear unrelated, had not a third species been discovered that exactly bridges the gap. Unfortunately the imago of the third species is unknown, and so it remains undescribed at present. However, its enteric valve is illustrated in Pl. 9, fig. 5, because of the phylogenetic interest of its intermediate structure. The

dimensional similarity of the two species is illustrated by their closeness in the plots of canonical variates (Text-figs 607 and 608) and of principal component scores (Text-fig. 610). The abdomen of the worker caste is dehiscent throughout the genus.

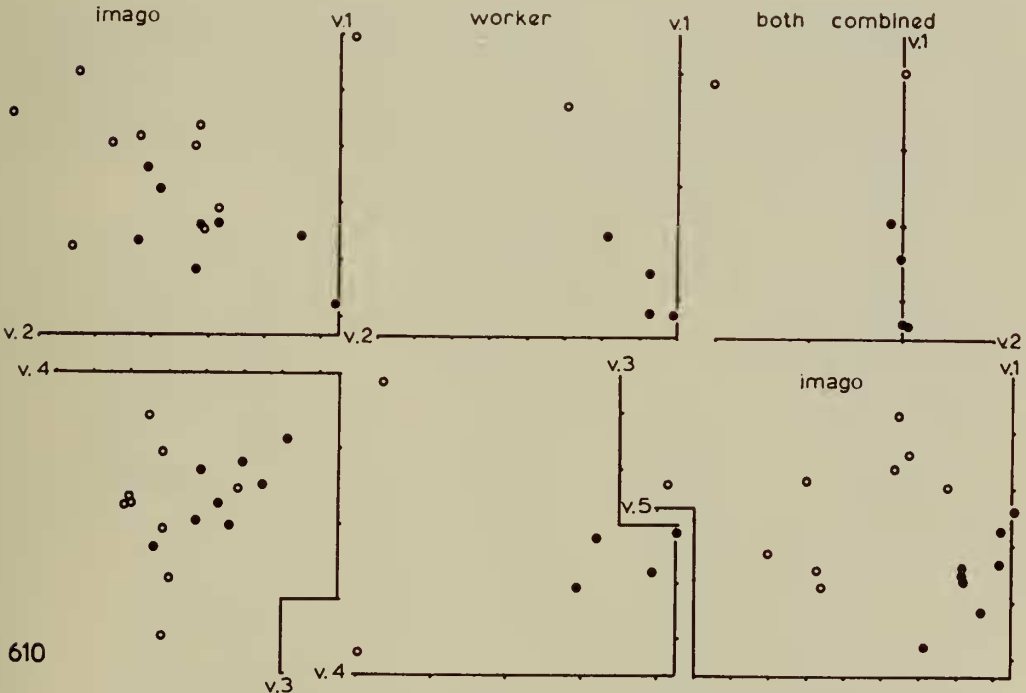
KEYS TO SPECIES

Imagos

- 1 Postclypeus slightly less inflated, Pcl/R_A , 1.82-2.45; complex ratio of mandible and notal measurements $L_1/M.N.$, 1.26-1.52. Abdominal stigmata usually paler than surrounding tergites and sternites. (Distribution, W. Africa, Nigeria to Gambia) *cavator* (p. 224)
- Postclypeus slightly more inflated, Pcl/R_A , 2.37-3.00; complex ratio $L_1/M.N.$, 1.50-2.05. Abdominal stigmata usually darker than surrounding sclerites. (Distribution, E. African, Uganda to N.E. Tanzania). *fossor* (p. 226)

Workers

- 1 Enteric valve with internal cushions retracted, distal ends armed with numerous prominent but fine spicules, and similar spicules on smooth membranous wall of valve between and beyond cushions; proximal parts of cushions smooth and



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FIG. 610. *Aderitotermes*, distinction between *A. cavator* (rings) and *A. fossor* (spots). Plots of principal component scores (transformed variables) corresponding to first to fourth latent roots of correlation matrices of worker and imago, first and second of both castes combined, and fifth of imago alone. Only on the fifth was there clear separation of imagos. The largest weighting coefficients of the fifth eigenvector attached to the meso- and metanotal widths, providing the complex discriminant ratio $L_1/M.N.$ used in the key.

unarmed. Apical teeth of mandibles shorter, L_A/L_1 , 0.60-0.64, R_A/R_1 , 0.78-0.88.

Fore tibia slightly swollen, T_1/T_w , 4.21-4.62 *fossor* (p. 226)

- Enteric valve with cushions produced through valve opening as flattened vanes, surface scaly, each scale fringed with minute spicules and a few small spines; membranous wall of valve between and beyond cushions carunculated, each lobe fringed distally with minute spicules. Apical teeth of mandibles longer, L_A/L_1 , 0.64-0.79, R_A/R_1 , 0.88-1.00. Fore tibia scarcely swollen, T_1/T_m , 5.08-5.31

cavator (p. 224)

Aderitotermes cavator sp. n.

(Text-figs 610, 611-614 & 619-624; Pl. 9, figs 6-9)

Imago. Head capsule dark sepia-brown, darker above ocelli, dark areas sometimes extending as streaks tapering towards fontanelle; fontanelle circular or very short oval, flat or slightly depressed, smaller than ocellus, yellow-white to yellow-brown, conspicuous; medial spot circular, flat, smaller than fontanelle, sepia-brown; postclypeus brown, labrum yellow-brown; frontal marks flat brown crescents; antennae yellow-brown; pronotum sepia-brown, meso- and metanota brown; femora pale yellow-brown, tibiae yellow, tarsi paler. Abdominal tergites sepia-brown, dorsal stigmata paler, sternites brown, yellow in middle, ventral stigmata pale brown; cerci pale yellow.

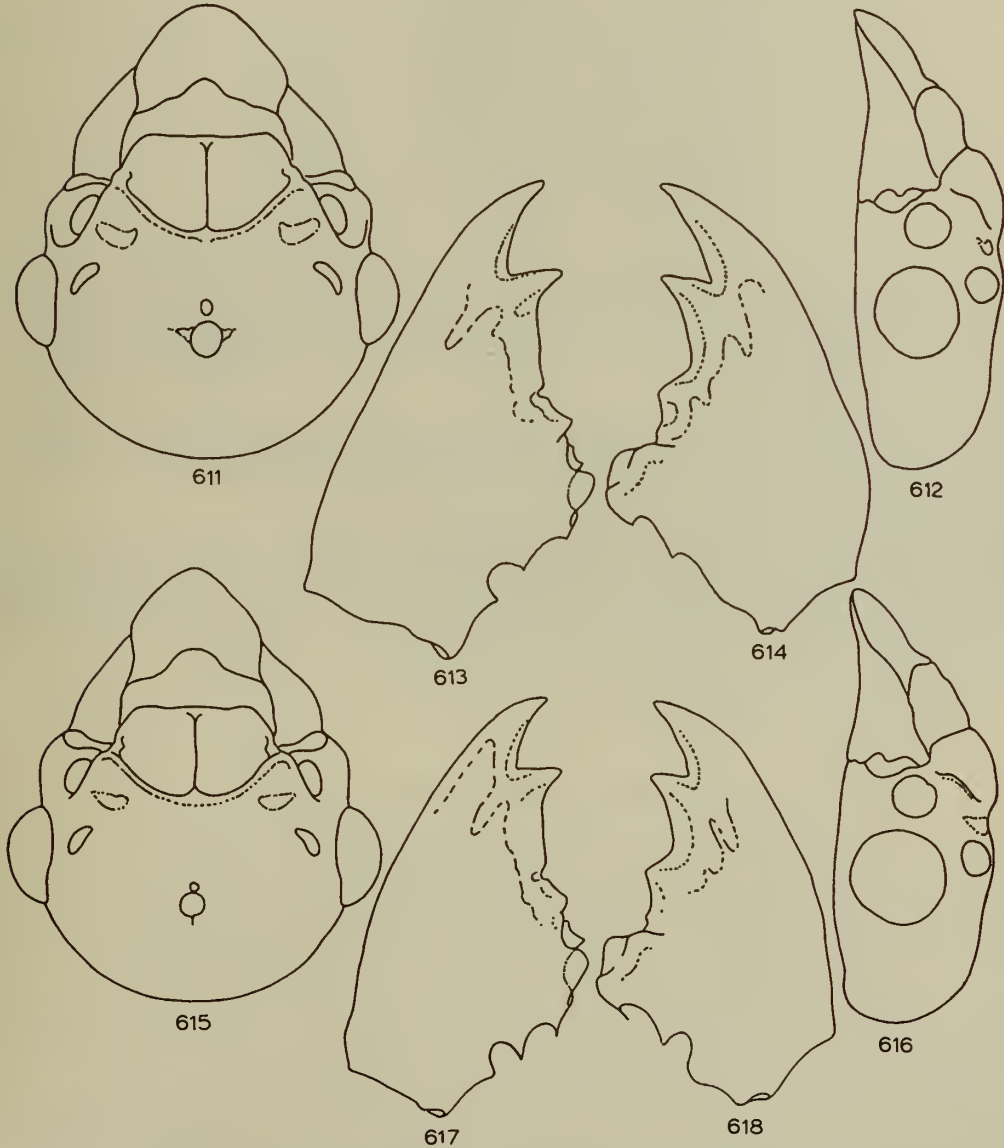
Posterior margin of head capsule usually slightly undulating not quite evenly rounded, but some specimens evenly rounded; ocelli fairly large, separated from compound eyes by half own least diameter or more; postclypeus weakly to moderately inflated, Pcl/W , 0.21-0.27, Pcl/R_A , 1.82-2.45, posterior margin arched or evenly rounded, median suture present, sometimes weak. Characters of mandibles and head pilosity given in generic diagnosis. Complex ratio of mandible and notal measurements $L_1/M.N.$, 1.26-1.52.

Measurements (nine specimens from five localities) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	1.09-1.31	1.213 \pm 0.072
Ocellus ($O_w \times O_l$)	0.09-0.13 \times 0.12-0.18	0.098 \pm 0.011 \times 0.137 \pm 0.019
Ocellus to eye (O-E)	0.05-0.09	0.070 \pm 0.013
Postclypeus length (Pcl)	0.25-0.33	0.293 \pm 0.030
Antennal article III	0.04-0.07	0.050 \pm 0.011
Antennal article IV	0.05-0.06	0.058 \pm 0.007
Antennal article V	0.05-0.07	0.060 \pm 0.008
Left mandible, apical to first marginal (L_A)	0.09-0.14	0.125 \pm 0.014
Left mandible, first to third marginal (L_1)	0.17-0.24	0.200 \pm 0.019
Left mandible, third marginal to molar (L_m)	0.07-0.09	0.081 \pm 0.006
Right mandible, apical to first marginal (R_A)	0.11-0.15	0.131 \pm 0.013
Right mandible, first to second marginal (R_1)	0.14-0.18	0.150 \pm 0.016
Right mandible, second marginal to molar (R_m)	0.07-0.09	0.081 \pm 0.009
Metanotum width (M)	0.35-0.42	0.386 \pm 0.027
Metanotum width (N)	0.38-0.44	0.397 \pm 0.023

Worker. Head capsule yellow-white, pilosity pale yellow, very sparse. Postclypeus moderately inflated, Pcl/W , 0.26-0.28, Pcl/R_1 , 2.38-2.44. Apical teeth of mandibles rather long, L_A/L_1 , 0.64-0.79, R_A/R_1 , 0.88-1.00. Fore tibia scarcely swollen, T_1/T_w , 5.08-5.31. Enteric

valve seating connected to second pouch of proctodeum by a very distinct neck of moderate length; internal cushions of enteric valve all produced through valve opening as flattened vanes, their surfaces reticulated or scaly, posterior margin of each scale fringed with minute spicules and one or two small spines; membranous wall of valve between and beyond cushions carunculated, each lobe fringed posteriorly with very numerous minute spicules. Other characters of mandibles and intestine given in generic diagnosis.



FIGS 611-618. *Aderitotermes*, imago head capsules, front and side views, and imago mandibles. 611-614, *A. cavator*; 615-618, *A. fossor*.

Measurements (two specimens from separate localities) in millimetres.

Head width (W)	0.98-0.99
Fore tibia width (T_w)	0.15-0.16
Fore tibia length (T_1)	0.76-0.86
Postclypeus length (Pcl)	0.25-0.28
Left mandible, apical to first marginal (L_A)	0.09-0.12
Left mandible, apical to third marginal (L_1)	0.15-0.17
Left mandible, third marginal to molar (L_m)	0.06-0.07
Right mandible, apical to first marginal (R_A)	0.09-0.11
Right mandible, first to second marginal (R_1)	0.11-0.13
Right mandible, second marginal to molar (R_m)	0.06-0.08

A. cavator is the more specialized of the two described species, and the third known species is intermediate in form between *A. cavator* and the type-species of the genus, *A. fossor*. The longer apical teeth of the mandibles, and the varied enteric valve armature are characteristic.

Holotype ♀ (queen), paratype ♂ (king) and workers from type-colony, NIGERIA: Northern Region, Samaru, near Zaria, xii.1958 (*W. A. Sands* coll., No. S.2142) in British Museum (Natural History).

Other paratype material. NIGERIA: Northern Region: 30 m. from Lokoja, on Okene Road, 8.iii.1958, Samaru, 18.v.1959 (*W. A. Sands*); Eastern Region, Port Harcourt, 19.x.1957 (*W. Wilkinson*). IVORY COAST: Mount Nimba, Yale, 14.iv.1968 (*G. Josens*). GAMBIA: Nyambai, 16°40'W., 13°18'N., 13.ix.1966 and between Sanyang and Gunjur, 16°46'W., 13°15'N., 16.ix.1966 (*W. A. Sands*).

This species was recorded from soil, the foot of trees, and *Macrotermes* mounds.

Aderitotermes fossor sp. n.

(Text-figs 610, 615-618 & 625-630; Pl. 9, figs 1-4)

Imago. Head capsule sepia-brown or tinged with reddish towards chestnut-brown, darker above ocelli, dark areas sometimes extending as streaks towards fontanelle; fontanelle circular, flat, about half as large as ocellus, yellow-white, very conspicuous; medial spot oval, flat, smaller than fontanelle, coloured as head; postclypeus brown, labrum yellow-brown; frontal marks weakly developed flat crescents, coloured as head or slightly paler; antennae pale yellow-brown. Pronotum sepia-brown, meso- and metanota brown; femora pale yellow-brown, tibiae and tarsi paler. Abdominal tergites brown, dorsal stigmata dark sepia-brown, sternites pale brown, yellow in middle, ventral stigmata brown; cerci yellow.

Posterior margin of head capsule evenly rounded; ocelli medium-sized, separated from compound eyes by half own least diameter or more; postclypeus weakly to moderately inflated, Pcl/W, 0.24-0.30, Pcl/ R_A , 2.37-3.00, posterior margin evenly rounded, median suture distinct, characters of mandibles and head pilosity given in generic diagnosis. Complex ratio of mandible and notal measurements, $L_1/M.N$, 1.50-2.05.

Measurements (eight specimens from four localities) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	1.04-1.21	1.125 \pm 0.055
Ocellus ($O_w \times O_l$)	0.08-0.10 \times 0.10-0.13	0.091 \pm 0.009 \times 0.118 \pm 0.011
Ocellus to eye (O-E)	0.05-0.08	0.064 \pm 0.010
Postclypeus length (Pcl)	0.27-0.34	0.291 \pm 0.022
Antennal article III	0.03-0.06	0.044 \pm 0.008
Antennal article IV	0.04-0.06	0.051 \pm 0.006
Antennal article V	0.04-0.06	0.049 \pm 0.005
Left mandible, apical to first marginal (L_A)	0.10-0.11	0.106 \pm 0.005
Left mandible, first to third marginal (L_1)	0.18-0.19	0.182 \pm 0.007
Left mandible, third marginal to molar (L_m)	0.06-0.08	0.076 \pm 0.006
Right mandible, apical to first marginal (R_A)	0.10-0.12	0.110 \pm 0.005
Right mandible, first to second marginal (R_1)	0.13-0.14	0.136 \pm 0.006
Right mandible, second marginal to molar (R_m)	0.06-0.09	0.078 \pm 0.008
Mesonotum width (M)	0.29-0.35	0.326 \pm 0.022
Metanotum width (N)	0.30-0.36	0.334 \pm 0.022

Worker. Head capsule yellow-white, pilosity pale yellow, very sparse. Postclypeus moderately inflated, Pcl/W, 0.25-0.27, Pcl/ R_1 , 2.22-2.35. Apical teeth of mandibles short, L_A/L_1 , 0.60-0.64, R_A/R_1 , 0.78-0.88. Fore tibia slightly swollen, T_1/T_w , 4.21-4.62. Enteric valve seating connected to second pouch of proctodeum by very long neck; internal cushions of enteric valve all retracted, equally developed, armed at posterior ends with numerous long, prominent but fine spicules, rest of cushions smooth and unarmed; membranous wall of valve between and beyond cushions similarly armed with long spicules forming an entire fringe round valve opening. Other characters of mandibles and intestine given in generic diagnosis.

Measurements (four specimens from four localities) in millimetres.

	Range	Mean
Head width (W)	0.90-0.95	0.916
Fore tibia width (T_w)	—	0.148
Fore tibia length (T_1)	0.63-0.68	0.642
Postclypeus length (Pcl)	0.23-0.25	0.239
Left mandible, apical to first marginal (L_A)	—	0.089
Left mandible, first to third marginal (L_1)	0.14-0.15	0.144
Left mandible, third marginal to molar (L_m)	0.04-0.05	0.048
Right mandible, apical to first marginal (R_A)	—	0.088
Right mandible, first to second marginal (R_1)	0.10-0.11	0.105
Right mandible, second marginal to molar (R_m)	0.05-0.06	0.053

A. fossor was chosen as type-species of the genus *Aderitotermes* because although quite distinct from other genera, it is the most primitive in having shorter apical mandibular teeth, and the enteric valve armature of spicules alone. It shows distinct resemblances to *Amicotermes* in this respect, and it should be noted that a dense fringe of minute spicules is also found in *Acholotermes*. Both these genera have more elongated apical teeth, but the enteric valve seating is similar, and in

A. epius there is a tendency for it to move into a dorsal position accompanied by an elongation of the mesenteric-proctodeal overlap.

Holotype ♀ imago, paratype ♂ and ♀ imagos, and workers from type-colony, UGANDA: Kampala, Makerere, 27.1959 (*A. French*), in British Museum (Natural History).

Other paratype material. UGANDA: Kawanda, v.1949 (*W. V. Harris*); Bubandi, 1952 (*H. A. Osmaston*). KENYA: Kisumu, 15.vii.1940 (*E. E. Haviland*) in AMNH; Kiamosi Forest, Kakamega District, 20.iv.1952 (*W. A. Sands*). TANZANIA: Amani, Lewa, 14.iii.1951 and Ngua, 7.viii.1951 (*P. B. Kemp*). ZAMBIA: Abercorn, iii.1947 (*P. E. Glover*). MALAWI: 9 m. N. of Kota-Kota turnoff on Dowa-Lilongwe Road, 16.ix.1953 (*W. Sands & W. Wilkinson*). All material in British Museum (Natural History) unless otherwise stated.

This species appears to be one in which the alate swarms emerge in daylight, and has several times been collected in the act. It is also recorded walking about above ground level when expelled by doryline ants in the same way as *Alyscotermes kilimandjaricus*. Other records have been from small grassy mounds in forest glades.



FIGS 619-630. *Aderitotermes*, worker mandibles, mesenteric-proctodeal junctions showing attachments of malpighian tubules and positions of malpighian knot, and views of enteric valve seating. 619-624, *A. cavator*; 625-630, *A. fossor*.

ADAIPHROTERMES gen. n.

(A—'Not', daiphron, Gr., 'warlike')

Type-species: *Adaiphrotermes cuniculator* sp. n.

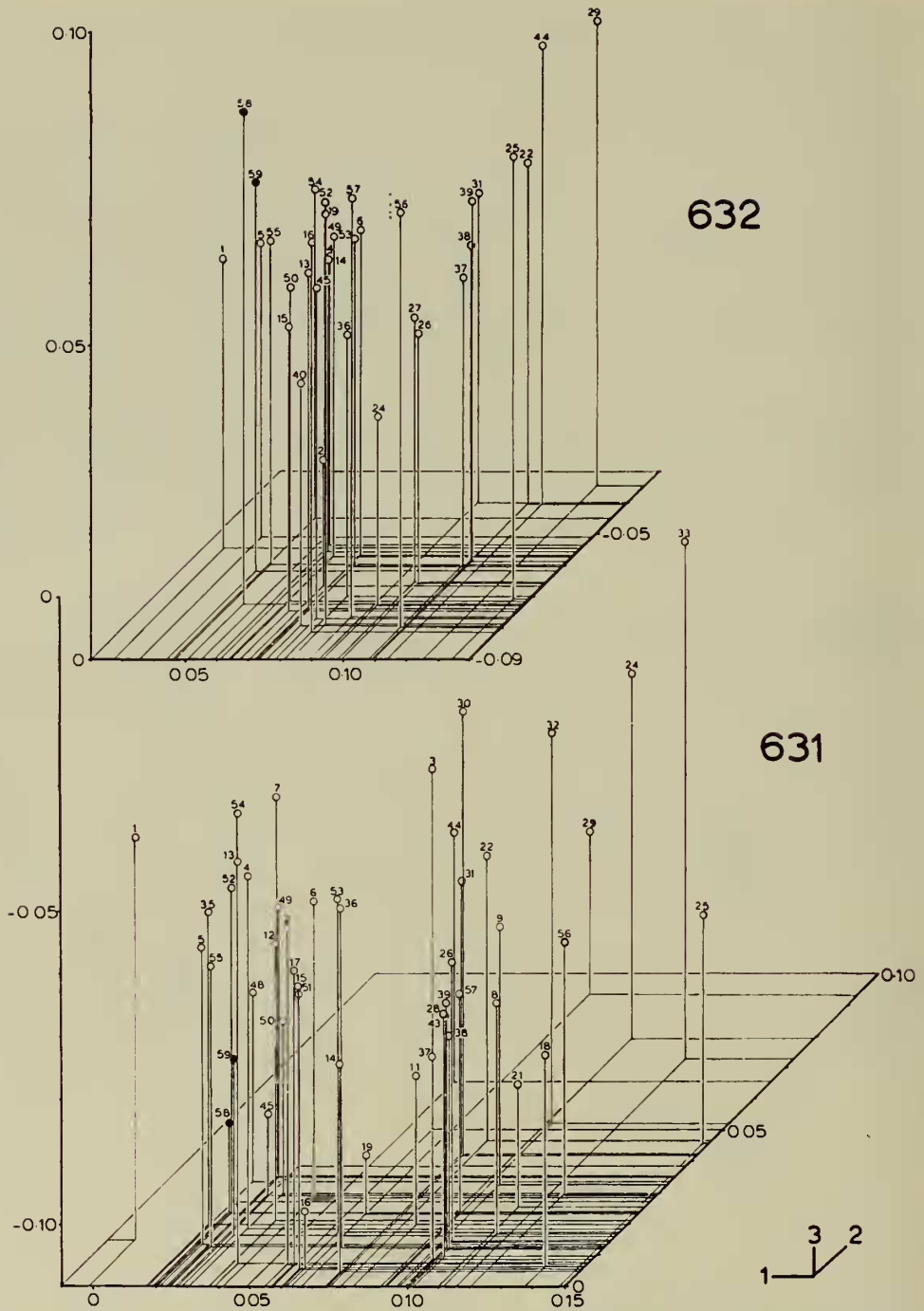
Imago. Small to medium-sized, W, 0.71–1.01. Fore tibia with only two apical spurs. Apical teeth of mandibles short, L_A/L_1 , 0.43–0.57, complex ratio, R_A/R_1 , 0.66–0.93; subsidiary marginal tooth of left mandible with proximal end, clear of molar prominence in surface view, complex ratio, $L_A/L_1.L_m$, 5.96–11.10. Right mandible with first and second marginal teeth more or less equal in length and in line with apical tooth. Meso- and metanota narrow at constriction, M/W, 0.16–0.23; mesonotal suture absent, metanotal suture weak or absent.

Worker. Small to medium-sized, W, 0.59–0.75. Fore tibia with only two apical spurs, hairy, with prominent bristles on posterior margin, swollen, T_1/T_w , 3.00–4.00. Apical teeth of mandibles short, L_A/L_1 , 0.46–0.64, R_A/R_1 , 0.65–1.10; subsidiary marginal tooth of left mandible with proximal end clear of molar prominence, complex ratio, $L_A/L_1.L_m$, 10.1–14.3; apical and marginal teeth of right mandible approximately equal and with their points in line, complex ratio, $R_A/R_1.R_m$, 14.3–20.8. Mixed segment of gut (mesenteric overlap with proctodeum) elongated extending beyond malpighian knot, mesenteron terminating in spherical or hemispherical dilation. First section of proctodeum long, swollen, constricting sharply to narrow tubular enteric valve; valve seating with two or three lobes or a simple rim, sessile on second pouch of proctodeum or with short neck, dorsal in position in unopened abdomen; internal cushions of enteric valve unarmed, reticulate or weakly scaled, mainly towards proximal ends.

The characters given in the above diagnosis make this one of the easiest genera to recognize. No other African genus completely lacks the third apical spur on the fore tibia, and in the worker caste the very characteristic gut with the white mesenteric 'ball' is easily recognizable even in the unopened abdomen. The abdomen of the worker is not dehiscent in this genus. The only other genera with an elongated mixed segment are *Aderitotermes* and *Anenteotermes*, and in these the end of the mesenteron is not dilated. In the multivariate analyses based on measurements, *Adaiphrotermes* stands out more clearly (Text-figs 631 and 632) than in the vector diagram of the similarity analysis (Text-fig. 633), but in all it is close to the large *Astalotermes*-*Anenteotermes* cluster as previously stated. Outside Africa, the most closely similar genus appears to be the Neotropical *Anoplotermes*, which also has only two apical spurs on the fore tibia, and a closely similar gut. However, the proportions of the apical and marginal teeth of the mandibles are different, and the proximal end of the subsidiary marginal tooth of the left mandible is hidden well behind the molar prominence. This is a feature of most of the more primitive genera of the Oriental region, and of most termites, and is far more important than its relative size would suggest. There is little doubt that the *Anoplotermes* of South America actually comprise several genera as do the African species hitherto also all included in that genus, and that the similarities result from convergence rather than close direct relationship.

Only three species are described in *Adaiphrotermes*, but worker castes alone of several other species are also known. However it is considered undesirable at present to describe them in the absence of their corresponding imago castes.

Adaiphrotermes appears to be the only genus which has definitely been recorded as attacking sound wood, though it is unlikely that this is its main diet. Both *A. choanensis* and *A. scapheutes* have been found on bait pegs in 'graveyard' tests in South Africa and Zambia.



FIGS 631 & 632. Three-dimensional graphs of canonical variates 1, 2, & 3 showing species of *Adaiphrotermes* as solid spots. 631, imago, 632, worker caste.

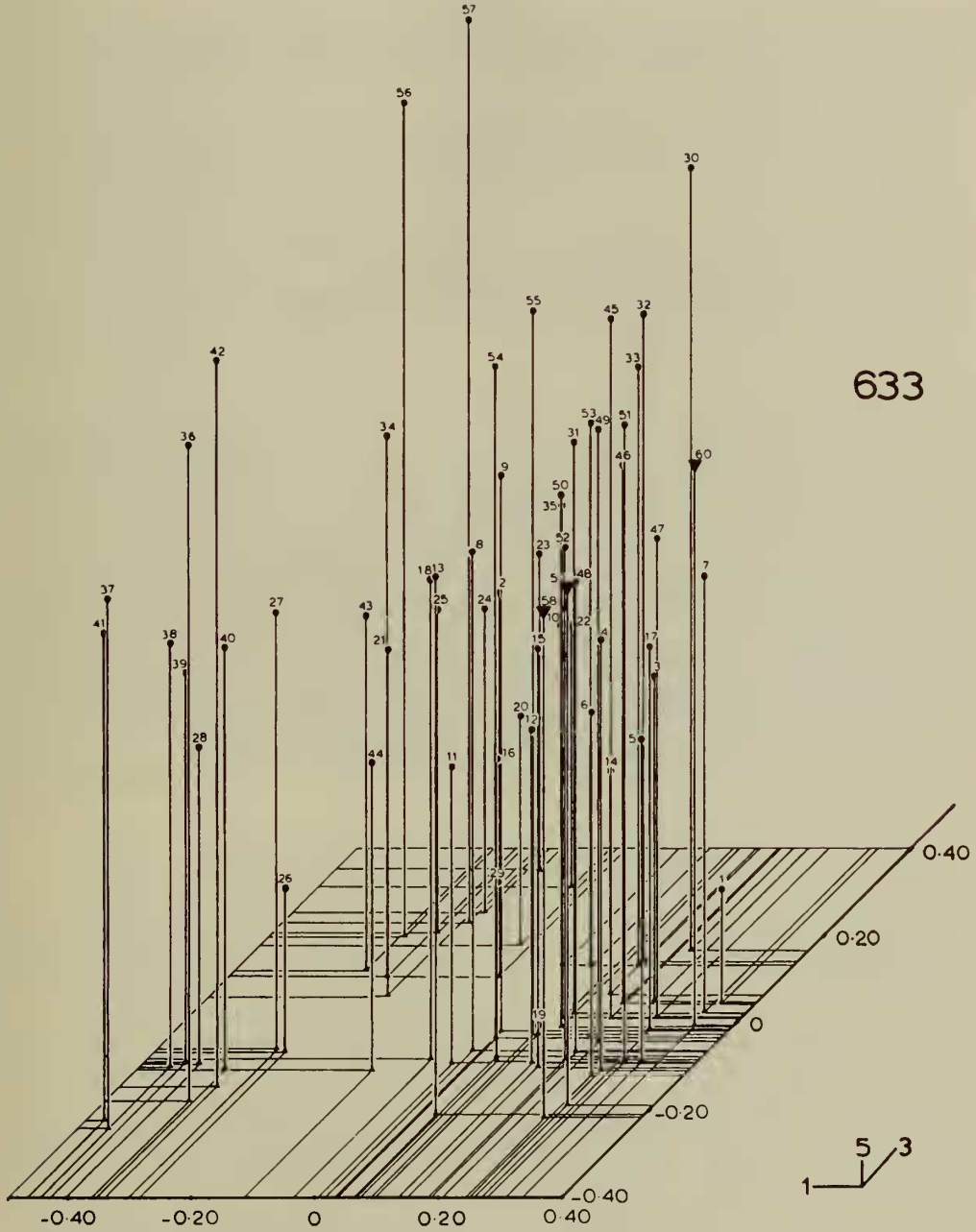


FIG. 633. Three-dimensional graph of principal co-ordinates analysis-plot of eigenvectors 1, 3 & 5 showing species of *Adaiptertermes* marked by large triangles.

KEYS TO SPECIES

Imagos

- 1 Fontanelle small to vestigial, short oval to circular, flat or slightly depressed, equal in size to or smaller than medial spot, distinct and pale coloured to obscure, coloured as head. Larger, W, 0.83-1.01 2
- Fontanelle usually large, oval to elongate oval, pale and sharply distinct from head colour, larger than medial spot and often slightly raised; small specimens, W under 0.80, may have small inconspicuous fontanelle. Distribution, S. Africa to Tanzania *choanensis* (p. 232)
- 2 Postclypeus moderately to strongly inflated, with evenly rounded posterior margin and distinct median suture, Pcl/R_A, 2.88-3.31; posterior margin of head capsule unevenly rounded (Text-fig. 638) *cuniculator* (p. 235)
- Postclypeus strongly inflated with sinuate posterior margin and weak or indistinct median suture, Pcl/R_A, 3.59; posterior margin of head capsule evenly rounded *scapheutes* (p. 237)

Workers

- 1 Length of mixed segment, measured round outside of curve, 3-4 times width of mesenteron at insertion of malpighian tubules *cuniculator* (p. 235)
- Length of mixed segment, measured round outside of curve, more than five times width of mesenteron at insertion of malpighian tubules 2
- 2 Left mandible with proximal end of subsidiary marginal tooth well clear of molar prominence; enteric valve seating with three definite lobes and a short neck connecting it to proctodeal pouch; postclypeus less inflated, Pcl/R₁, 1.59, apical teeth of mandibles shorter, L_A/L₁, 0.46, R_A/R₁, 0.65. Fore tibia more inflated, T₁/T_w, 3.08 *scapheutes* (p. 237)
- Left mandible with proximal end of subsidiary marginal tooth only just clear of molar prominence; enteric valve seating a circular rim or weakly lobed, sessile on proctodeal pouch; postclypeus more inflated, Pcl/R₁, 2.50-3.40; apical teeth of mandibles longer, L_A/L₁, 0.50-0.64, R_A/R₁, 0.70-1.10; fore tibia less inflated, T₁/T_w, 3.52-4.00. (Most of these characters also apply to *cuniculator*.) *choanensis* (p. 232)

Adaphrotermes choanensis (Fuller) comb. n.

(Text-figs 634-637 & 646-650; Pl. 9, fig. 10)

Mirotermes (*Procutitermes*) *choanensis* Fuller, 1925: 184. LECTOTYPE ♀, REPUBLIC OF SOUTH AFRICA: Pretoria, Arcadia (National Collection of Isoptera, Pretoria) here designated [examined].

Imago. Head capsule varies from sepia-brown to dark sepia-brown, pitch-black above ocelli; fontanelle from very small, circular, slightly depressed and coloured as head, to larger than ocelli, white, swollen, elongate oval; medial spot circular to oval about one-quarter size of ocellus, usually slightly raised; postclypeus sepia-brown, labrum yellow-brown; frontal marks variable, usually distinct, crescent-shaped, without setae, flat; antennae pale brown. Pronotum sepia-brown, meso- and metanota brown, without dark sutures; legs, femora and tibia brown, tarsi, pale yellow. Abdominal tergites sepia-brown, dorsal stigmata pale brown; sternites brown, paler in mid-line, ventral stigmata also brown; cerci yellowish white.

Posterior margin of head capsule evenly rounded; ocelli medium-sized, separated from compound eyes by half to two-thirds own least diameter; postclypeus medium-sized to large and moderately inflated, Pcl/W, 0.20-0.30, hind margin evenly rounded, median suture distinct.

Pilosity of head capsule somewhat uneven with many long setae, not quite forming a pelt, brown.

Measurements (23 specimens from 14 localities) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	0.71-0.96	0.872 \pm 0.063
Ocellus ($O_w \times O_l$)	0.06-0.09 \times 0.08-0.12	0.072 \pm 0.007 \times 0.095 \pm 0.010
Ocellus to eye (O-E)	0.03-0.06	0.044 \pm 0.009
Postclypeus length (Pcl)	0.18-0.25	0.222 \pm 0.021
Antennal article III	0.01-0.03	0.015 \pm 0.004
Antennal article IV	0.03-0.05	0.032 \pm 0.006
Antennal article V	0.02-0.04	0.030 \pm 0.006
Left mandible, apical to first marginal (L_A)	0.05-0.08	0.067 \pm 0.009
Left mandible, first to third marginal (L_1)	0.09-0.15	0.131 \pm 0.016
Left mandible, third marginal to molar (L_m)	0.05-0.07	0.061 \pm 0.006
Right mandible, apical to first marginal (R_A)	0.05-0.08	0.073 \pm 0.009
Right mandible, first to second marginal (R_1)	0.07-0.10	0.091 \pm 0.010
Right mandible, second marginal to molar (R_m)	0.05-0.08	0.065 \pm 0.007
Mesonotum width (M)	0.13-0.21	0.176 \pm 0.024
Metanotum width (N)	0.14-0.21	0.182 \pm 0.020

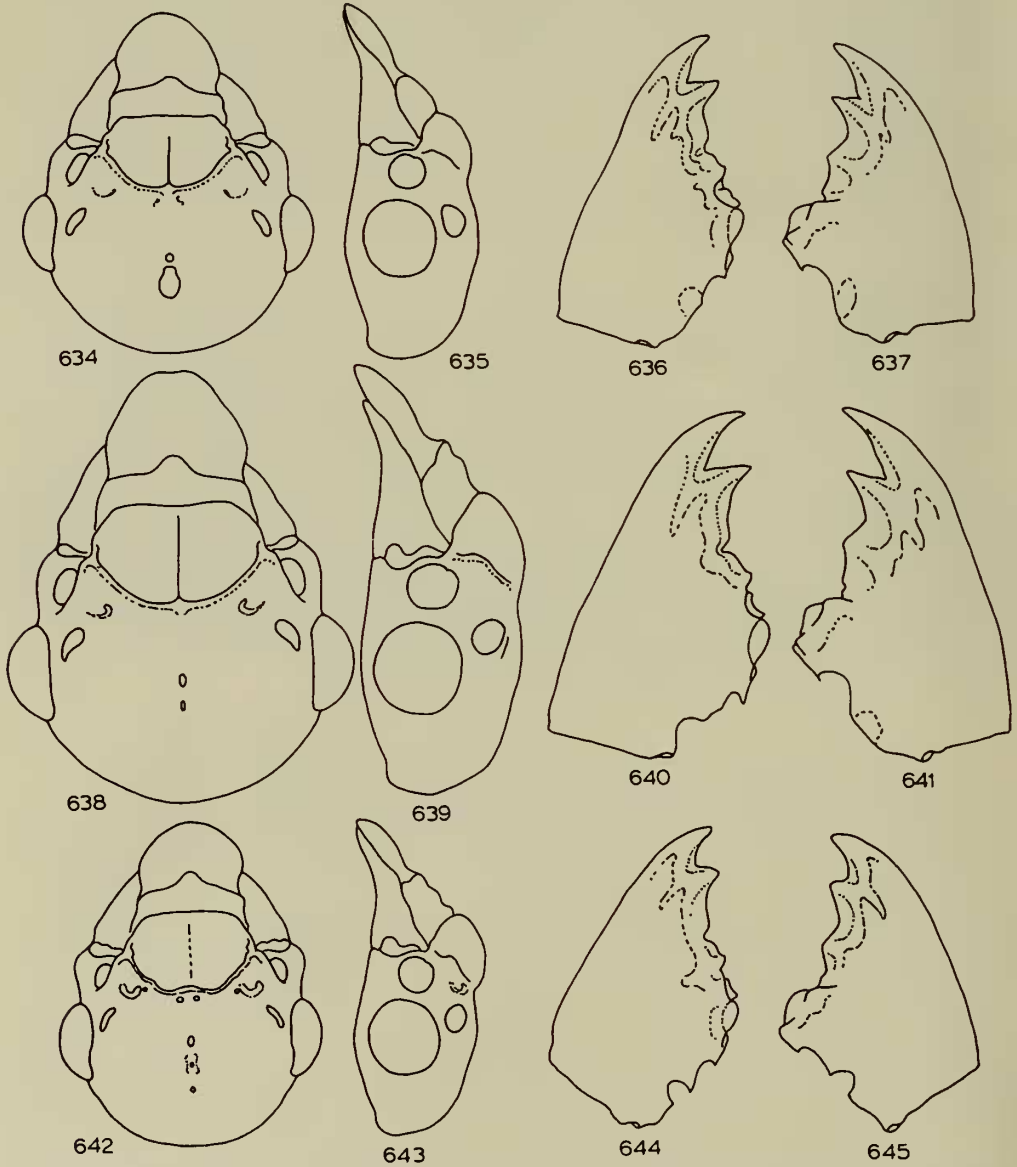
Worker. Head capsule white, pilosity short and fine, pale yellow. Postclypeus moderately inflated, Pcl/ R_1 , 2.50-3.40, Pcl/W, 0.27-0.34; left mandible with proximal end of subsidiary marginal tooth just clear of molar prominence. Fore tibia inflated, T_1/T_w , 3.54-4.00. Mixed segment of gut very long, length 7-8 times width of mesenteron at insertion of malpighian tubules; enteric valve seating a sessile circular rim on second pouch of proctodeum, completely hidden under folds of rectum in dorsal view of abdomen; internal cushions smooth with no trace of scales or reticulations, membrane beyond cushions with vestigial spicules.

Measurements (nine specimens from nine localities) in millimetres.

	Range	Mean \pm S.D.
Head width (W)	0.59-0.73	0.627 \pm 0.049
Fore tibia width (T_w)	0.12-0.14	0.129 \pm 0.006
Fore tibia length (T_1)	0.44-0.53	0.488 \pm 0.027
Postclypeus length (Pcl)	0.18-0.24	0.202 \pm 0.021
Left mandible, apical to first marginal (L_A)	0.05-0.07	0.059 \pm 0.007
Left mandible, first to third marginal (L_1)	0.09-0.11	0.102 \pm 0.007
Left mandible, third marginal to molar (L_m)	0.04-0.05	0.044 \pm 0.004
Right mandible, apical to first marginal (R_A)	0.04-0.07	0.059 \pm 0.008
Right mandible, first to second marginal (R_1)	0.06-0.08	0.067 \pm 0.005
Right mandible, second marginal to molar (R_m)	0.04-0.06	0.048 \pm 0.005

Adaiaphrotermes choanensis shows a remarkable degree of variation in the imago caste, such that it was at first divided into two species. However, intermediates between the forms were found and it became clear that the differences were associated with collections made in different years. It happened that the greater part of the material available for study was collected in batches of a number of nest-series from various localities in the years 1955, 1959, 1960 and 1962. There was a steady increase in size from the earlier to the later collections, coupled with an enlarging

fontanelle increasingly contrasting in colour with the darkening head, and progressing from depressed to protruding. At the same time the compound eyes remained relatively static, so that the head appeared more broadly rounded behind them, and they appeared to protrude less. Thus the species seemed to be evolving rapidly, until specimens collected in 1939 were examined and found to resemble the



FIGS 634-645. *Adaiaphrotermes*, imago head capsule, front and side views, and imago mandibles. 634-637, *A. choanensis*; 638-641, *A. cuniculator*; 642-645, *A. scapheutes* (mandibles worn).

later form. The only explanation that suggests itself is that of climatic fluctuations affecting the food supply. The smaller, paler coloured specimens with a flat or depressed fontanelle might occur in adverse conditions that recur from time to time. The 'typical' form is therefore likely to be the larger, darker version with a conspicuous raised fontanelle that separates it clearly from *Adaioprotermes cuniculator* and *Adaioprotermes scapheutes*. In the worker caste, the fore tibia is slightly less inflated, but the gut characters appear to be more specialized (cf. section on phylogeny).

That *A. choanensis* belonged to the soldierless termites was first recognized by Dr A. E. Emerson, who labelled the syntypes as *Anoplotermes*, thereby ensuring their inclusion here. The species was placed in the genus *Procutitermes* Silvestri by Snyder (1949: 167). It should be noted that Fuller associated a soldier of the genus *Lepidotermes* with the alates described under the name *Microtermes (Procutitermes) choanensis*, and the same vial, that is, the syntype series, included an imago of a species of *Astalotermes*. These specimens have been separated from the lectotype and paralectotypes of *A. choanensis*. The single soldier of *Lepidotermes* is not named here as this would require comparative studies of existing species, to one of which it may well belong.

A lectotype is designated below from the existing syntype material.

Type-material. *Mirotermes (Procutitermes) choanensis* Fuller, LECTOTYPE ♀ imago and paralectotype ♂ imagos from type-colony, REPUBLIC OF SOUTH AFRICA: Transvaal, Pretoria, Arcadia, 23.xi.1914 (*C. Fuller*), in National Collection of Isoptera, Pretoria; other paralectotypes from same colony in AMNH.

Other material. TANZANIA: Amani, Lewe, 14.iii.1951 (*P. B. Kemp*). MALAWI: Fort Lister Gap, 15°49'S., 35°51'E., 21.viii.1953 (*W. A. Sands & W. Wilkinson*). RHODESIA: Rekomitjie, 16°07'S., 29°24'E., 22.xi.1964 (two vials), Matopos, 20°25'S., 28°30'E., 17.xi.1965 and 22.xi.1965 (two vials) (*M. G. Bingham*). SWAZILAND: Stegi, 24.x.1960 (*J. L. Sheasby*); Hlatikulu, 25.x.1960 (*W. G. H. Coaton*), N.C.I. REPUBLIC OF SOUTH AFRICA: Transvaal, Pretoria, 27.x.1939 (three vials), Piet Retief, 7.xii.1959, Middleburg, 28.x.1960 (*W. G. H. Coaton*), N.C.I. and BMNH; Pretoria, 6.xi.1914 (*C. Fuller*), N.C.I. and AMNH; Natal, Zululand, Eshowe, 22.iv.1926 (*R. E. Turner*); Ubombo, 18.xi and 19.xi.1955 (five vials), Ingwavuma, 22.xi and 23.xi.1955 (three vials), Lower Tugela, 28.x.1957 (three vials), Ubombo, 8.xii and 18.xii.1959 (two vials), Ingwavuma, 14.xii.1959 (two vials) (*W. G. H. Coaton*), BMNH and N.C.I.; Ngotshe, 5.xii.1959, Vryheid, 5.xii.1959, Babanango, 6.xii.1959 (*P. C. Joubert*); Vryheid, 9.i.1962, Ubombo, 11.i.1962, Hlabisa, 11.i.1962, Entonjaneni, 13.i.1962 (*J. L. Sheasby*) BMNH and N.C.I.

Thirty-nine nest-series were examined, and the material is in the British Museum (Natural History) unless otherwise stated. In spite of the number of records available, nothing is known of the biology of this species.

Adaioprotermes cuniculator sp. n.

(Text-figs 638-641 & 651-655; Pl. 9, fig. 11)

Imago. Head capsule dark sepia-brown, darker above ocelli; fontanelle small or vestigial, circular, slightly depressed, from distinct and pale coloured to obscure, coloured as head;

medial spot, dark sepia-brown, oval, flat, equal in size or larger than fontanelle; postclypeus sepia-brown, labrum yellow-brown; frontal marks indistinct, flat, coloured as head; antennae, pale brown, pronotum, sepia-brown, meso- and metanota pale brown, without dark sutures; legs, femora and tibiae pale brown, tarsi, yellowish-white. Abdominal tergites, sepia-brown, dorsal stigmata yellowish white; sternites, brown laterally, very pale brown in middle, ventral stigmata, as dorsal, cerci, yellowish white.

Posterior margin of head capsule slightly unevenly rounded; ocelli medium-sized, separated from compound eyes by about two-thirds own least diameter; postclypeus large and moderately inflated, Pcl/W index, 0.25-0.30, hind margin evenly rounded, median suture distinct.

Pilosity of head capsule uneven with many long setae, not forming a pelt, brown.

Measurements (13 specimens from seven localities) in millimetres.

	Range	Mean \pm S.D.
Head width across eyes (W)	0.84-1.01	0.922 \pm 0.061
Ocellus ($O_w \times O_l$)	0.06-0.09 \times 0.09-0.13	0.076 \pm 0.011 \times 0.101 \pm 0.012
Ocellus to eye (O-E)	0.04-0.06	0.052 \pm 0.006
Postclypeus length (Pcl)	0.21-0.30	0.264 \pm 0.028
Antennal article III	0.01-0.03	0.017 \pm 0.004
Antennal article IV	0.04-0.05	0.042 \pm 0.003
Antennal article V	0.03-0.04	0.039 \pm 0.003
Left mandible, apical to first marginal (L_A)	0.06-0.10	0.079 \pm 0.012
Left mandible, first to third marginal (L_1)	0.14-0.17	0.157 \pm 0.012
Left mandible, third marginal to molar (L_m)	0.06-0.08	0.072 \pm 0.007
Right mandible, apical to first marginal (R_A)	0.07-0.10	0.086 \pm 0.011
Right mandible, first to second marginal (R_1)	0.01-0.13	0.110 \pm 0.011
Right mandible, second marginal to molar (R_m)	0.06-0.08	0.074 \pm 0.005
Mesonotum width (M)	0.14-0.19	0.162 \pm 0.016
Metanotum width (N)	0.15-0.22	0.183 \pm 0.022

Worker. Head capsule yellowish white, setae fine short, yellow. Postclypeus moderately inflated, Pcl/ R_1 , 2.14-2.94. Pcl/W, 0.27-0.34; left mandible with proximal end of subsidiary marginal tooth just clear of molar prominence. Fore tibia strongly inflated, T_1/T_w , 3.33-3.70. Mixed segment of gut length 3-4 times width of mesenteron at insertion of malpighian tubules; enteric valve seating sessile on second pouch of proctodeum, weakly three lobed; internal cushions, proximally weakly scaly, distally reticulated, sometimes with very small marginal points; membrane beyond cushions with sparse rows of minute spicules.

Measurements (six specimens from six localities) in millimetres.

	Range	Mean \pm S.D.
Head width (W)	0.69-0.75	0.729 \pm 0.022
Fore tibia width (T_w)	0.14-0.15	0.149 \pm 0.003
Fore tibia length (T_1)	0.50-0.53	0.514 \pm 0.013
Postclypeus length (Pcl)	0.19-0.25	0.231 \pm 0.023
Left mandible, apical to first marginal (L_A)	0.06-0.08	0.070 \pm 0.006
Left mandible, first to third marginal (L_1)	0.11-0.13	0.120 \pm 0.005
Left mandible, third marginal to molar (L_m)	—	0.051 \pm 0.002
Right mandible, apical to first marginal (R_A)	0.06-0.08	0.071 \pm 0.006
Right mandible, first to second marginal (R_1)	—	0.088 \pm 0.003
Right mandible, second marginal to molar (R_m)	—	0.050 \pm 0.002

A. cuniculator is usually distinguishable from *A. choanensis* in the imago by the less conspicuous fontanelle and flat medial spot. In the worker caste, the much shorter mixed segment of the gut is the most characteristic feature. In the other species, *A. scapheutes*, the imago postclypeus has a sinuate hind margin, and the fontanelle is practically obsolete. The worker has a long mixed segment like *A. choanensis* but the enteric valve seating has a short neck and three definite lobes, the postclypeus is less inflated, and the fore tibia more so.

Holotype ♀ imago, paratype ♂ and ♀ imagos, and workers from type-colony, GHANA: 40 m. from Tumu on Lawra Road, 16.iii.1959 (*W. A. Sands*, Coll. No. S.2458), in British Museum (Natural History).

Other paratype material. GHANA: 60 m. north of Ejura on Tamale Road, three nest-series, 24.ii.1959, 55 m. from Tamale on Damongo Road, 3.iii.1959, 35 m. from Tamale on Yendi Road, two nest-series, 4.iii.1959, 40 m. from Tumu on Lawra Road, 16.iii.1959, 6 m. north of Wa on Lawra Road, 19.iii.1959, 52 m. south of Wa on Sawla Road, 20.iii.1959, 19 m. from Sawla on Damongo Road, 21.iii.1959, 12 m. from Damongo on Tamale Road, 24.iii.1959 (*W. A. Sands*); Aburi, 1926 (*W. H. Patterson*); Kumasi, 3.ii.1955 (*W. V. Harris*). GAMBIA: Abuko, 13°24'N., 16°39'W., 10.ix.1966, between Sanyang and Gunjur, 13°15'N., 16°46'W., 16.ix.1966, 35 m. from Bathurst on Manso Konko Road, 18.ix.1966 (*W. A. Sands*). NIGERIA: Mid-Western Region (Benin Province), Obanokoro, Sobo Plain, 8.i.1957 (*W. Wilkinson*); Northern Region, Samaru, near Zaria, 25.iv.1959 (*W. A. Sands*).

Nineteen nest-series of this species were examined and all the material is in the British Museum (Natural History).

Nearly all of the records are from the surface layers of mounds of other termites, mostly those of *Macrotermes* or *Odontotermes* but with a few others such as *Cubitermes* and *Trinervitermes*. It appears to be a savanna species with a fairly wide distribution in West Africa.

Adaiphrotermes scapheutes sp. n.

(Text-figs 642-645 & 656-661; Pl. 9, fig. 12)

Imago. Queen only known, colour therefore probably faded. Head capsule yellow-brown, brown above ocelli; fontanelle almost obsolete, minute, oval, flat, brown; medial spot larger than fontanelle, one-third diameter of ocellus, flat, yellow-brown; postclypeus pale yellow-brown, labrum yellow; frontal marks indistinct flat crescents, pale yellow-brown; antennae yellow. Pronotum, meso- and metanota, pale yellow-brown, mesonotal suture absent, metanotal suture present; legs, femora and tibiae yellow, tarsi yellowish white. Abdominal tergites pale yellow-brown, dorsal stigmata darker, yellow-brown; sternites, laterally yellow, paler in middle, ventral stigmata pale yellow-brown, cerci yellowish white.

Posterior margin of head capsule evenly rounded; ocelli medium-sized, separated from compound eyes by two-thirds own least diameter; postclypeus larger and rather strongly inflated, Pcl/W index 0.32, hind margin sinuate, not evenly rounded, median suture weak.

Pilosity of head capsule uneven, not forming a pelt, yellow.

Measurements (one specimen) in millimetres.

Head width across eyes (W)	0.83
Ocellus (O _w × O _l)	0.07 × 0.10

Ocellus to eye (O-E)	0·04
Postclypeus length (Pcl)	0·27
Antennal article III	0·02
Antennal article IV	0·03
Antennal article V	0·03
Left mandible, apical to first marginal (L _A)	0·06
Left mandible, first to third marginal (L ₁)	0·14
Left mandible, third marginal to molar (L _m)	0·06
Right mandible, apical to first marginal (R _A)	0·07
Right mandible, first to second marginal (R ₁)	0·09
Right mandible, second marginal to molar (R _m)	0·06
Mesonotum width (M)	0·16
Metanotum width (N)	0·16

Worker. Head capsule pale yellow, fine, short, rather numerous pilosity, yellow. Postclypeus rather weakly inflated, Pcl/R₁, 1·59, Pcl/W, 0·21; left mandible with proximal end of subsidiary marginal tooth separated from molar prominence by pronounced notch. Fore tibia strongly inflated, T₁/T_w, 3·08. Mixed segment of gut long, length 5–6 times width of mesenteron at insertion of malpighian tubules; enteric valve seating with three distinct equal lobes, and a short neck connecting it to second pouch of proctodeum; internal cushions entirely reticulated, membrane beyond cushions with vestigial spicules.

Measurements (one specimen) in millimetres.

Head width (W)	0·66
Fore tibia width (T _w)	0·16
Fore tibia length (T ₁)	0·48
Postclypeus length (Pcl)	0·14
Left mandible, apical to first marginal (L _A)	0·05
Left mandible, first to third marginal (L ₁)	0·11
Left mandible, third marginal to molar (L _m)	0·05
Right mandible, apical to first marginal (R _A)	0·06
Right mandible, first to second marginal (R ₁)	0·09
Right mandible, second marginal to molar (R _m)	0·05

Adaiphrotermes scapheutes may be expected to overlap in its distribution with *A. choanensis*, from which it differs in the imago by the sinuate posterior margin of the postclypeus and the inconspicuous fontanelle. The worker mandible differs, and the fore tibia is more strongly inflated. Comparison with *Adaiphrotermes cuniculator* is made in the discussion on that species.

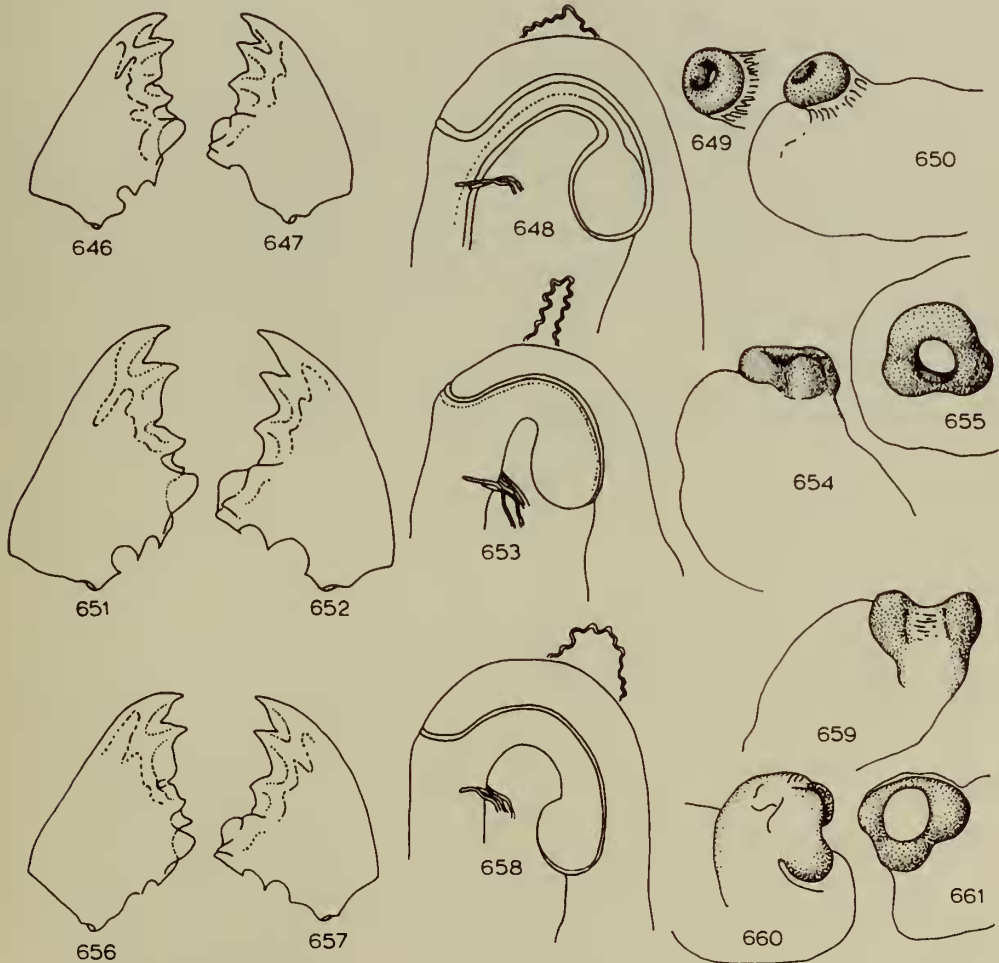
Holotype ♀, imago (queen) and three paratype workers from type-colony only, ZAMBIA: Kitwe, 23.i.1957 (*W. G. H. Coaton*) in National Collection of Isoptera, No. TM.3928, Pretoria.

Only the type-nest-series of this species is known. There is no information on its biology.

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FIGS 646-661. *Adaiphrotermes*, worker mandibles, mesenteric-proctodeal junctions showing attachments of malpighian tubules and positions of malpighian knot, and views of enteric valve seatings. 646-650, *A. choanensis*; 651-655, *A. cuniculator*; 656-661, *A. scapheutes*.

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APPENDIX

***Acholotermes socialis* (Sjöstedt) comb. n.**

Eutermes socialis Sjöstedt, 1899 : 38. LECTOTYPE ♀ imago, CAMEROUN: Mungo River (Naturhistoriska Riksmuseum, Stockholm), here designated [examined].

This species is catalogued in the genus *Pericapritermes* by Snyder (1949). Silvestri (1914) transferred it to *Anoplotermes* on the basis of specimens other than the type-series. Sjöstedt (1926) placed it in *Pericapritermes*, where it has remained, with the name in common use for a well known West African species. Emerson examined the remaining specimen of the type-series in the Sjöstedt collection in 1952 and labelled it as the lectotype of *Anoplotermes socialis* (Sjöstedt) but the designation has not been published until now.

This specimen was not examined until after the completion of the present work and too late for inclusion in the key to *Acholotermes*, to which it is now assigned. It agrees with *Acholotermes chirotus* in most of its measurements and complex ratios, and runs down to that species in the key. However, it differs in having a slightly longer postclypeus, a more elongate oval fontanelle, and larger ocelli. The lectotype specimen of *A. socialis* is broken into several pieces, the compound eyes are collapsed, and it is much faded from long preservation, adding to the difficulties of comparison. The more important worker caste is not available. In view of its poor condition, and the wide separation of the type-localities of the two species (1300

miles), it is inadvisable to synonymise *A. chirotus* with *A. socialis*. They may in future be proved synonymous by additional material from intermediate localities.

The specimen labelled as lectotype by Emerson in 1952 is so designated, as follows:-

Eutermes socialis Sjöstedt, LECTOTYPE ♀ imago, CAMEROUN: Mungo River, ix. 1874 (*R. Bucholz*), in Naturhistoriska Riksmuseum, Stockholm. (Sjöstedt reported also depositing specimens at Mus. Greifswald, E. Germany, but these have not been examined.)

The records of the species of *Pericapritermes* hitherto known as *P. socialis* are therefore misidentifications for which it is desirable to provide an alternative name. All the material identified as *P. socialis* at the BMNH has been compared with Sjöstedt's specimen of the soldier from CAMEROUN: Mungo River, x. 1874 (*R. Bucholz*) (Sjöstedt collection No. 931) and found to be the same species. This is the only species known from the forest areas around Lagos and Ibadan. Silvestri (1914) described *Pericapritermes urgens* Silvestri 'var. nov.' *nigeriana* as being smaller than the typical form. His localities were forests near Lagos, Olokemeji, and Ibadan. It is clear from his use of a geographical name that in this case his varietal concept should be construed as having subspecific rank. There is little doubt that this is the same species as that previously known as *P. socialis*, with which its description agrees in every particular. The name *nigeriana*, suitably emended, is available for the taxon, as set out below:-

***Pericapritermes nigerianus* Silvestri stat. n.**

Pericapritermes urgens Silvestri var. *nigeriana* Silvestri, 1914: 137. Syntype soldiers and workers, NIGERIA: Lagos, Olokemeji, Ibadan, in Silvestri Coll., Istituto Entomologia di Agraria, Naples.

All previously published uses of the erroneous combination *Pericapritermes socialis* (Sjöstedt) should now be referred to the above species name.

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(Junior synonyms are given in italics, species belonging to other groups in brackets).

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 retifaciens sp. n., 174

sanctus, 84
 scapheutes sp. n., 237
sedatus, 120
 sentosus sp. n., 176
 socialis, 242
 spinulatus sp. n., 179
 stolidus sp. n., 156

 tithasus sp. n., 149
 tranquillus, 181
 trestus sp. n., 133

warreni 84

PLATE I

Enteric valve armature. Some valves are mounted whole, others slit and opened out. Small 'p' in lower right corner indicates use of phase contrast illumination.

FIGS 1, *Acidnotermes praus*; 2, *Amalotermes phaeocephalus*; 3, *Astalotermes benignus*; 4, *Astalotermes amicus*; 5, *Astalotermes ignavus*; 6, *Astalotermes acholus*; 7, *Astalotermes brevior*; 8, *Astalotermes quietus*; 9, *Astalotermes empodius*; 10, *Astalotermes irrixosus*; 11, *Adynatotermes moretelae*.



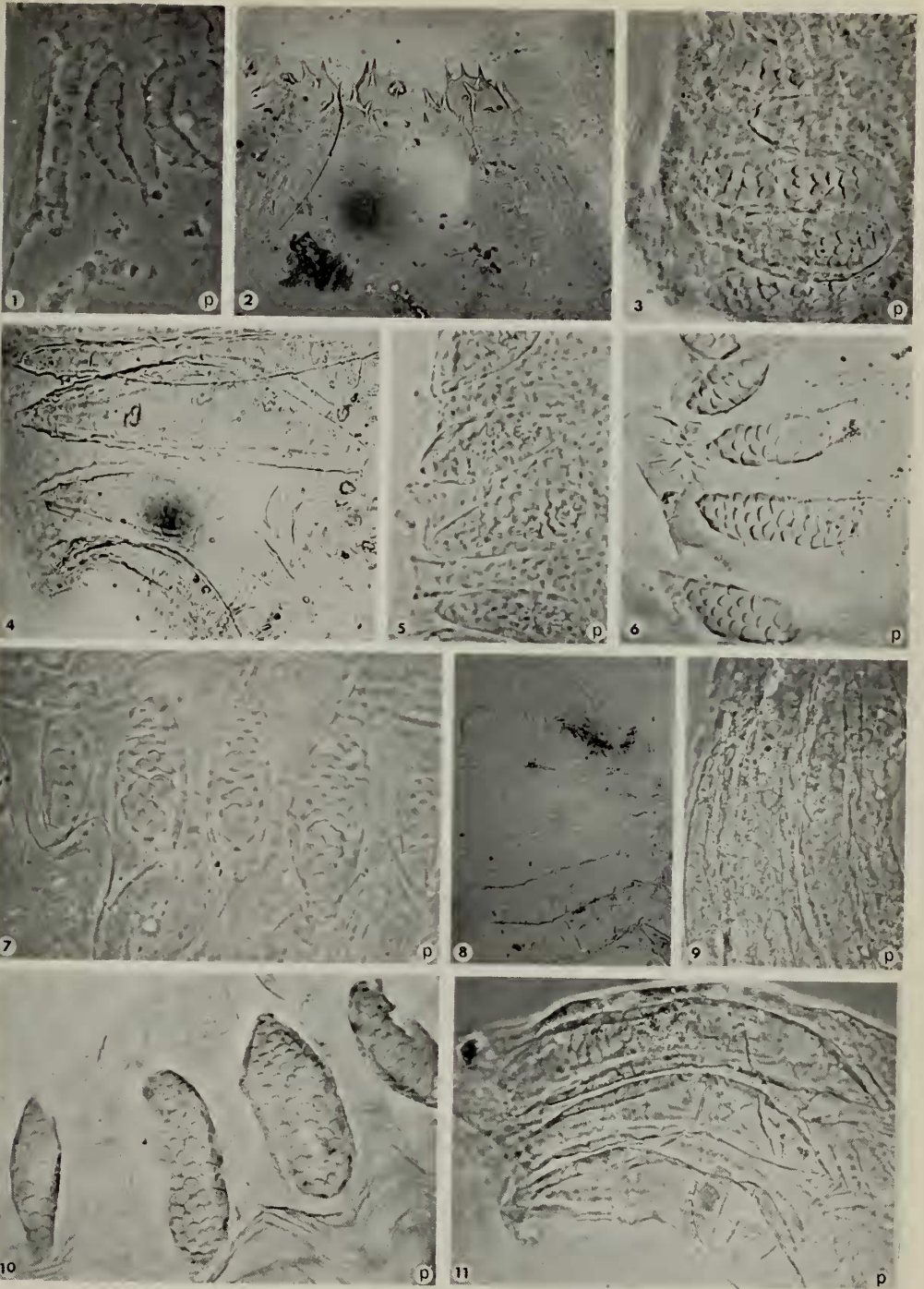


PLATE 2

Enteric valve armature. Some valves are mounted whole and viewed from side or end on, others slit and opened out. Small 'p' in lower right corner indicates use of phase contrast illumination.

FIGS 1, *Astratotermes aneristus*; 2, *Astratotermes hilarus*; 3, *Astratotermes pacatus*; 4, *Astratotermes mansuetus*; 5, *Astratotermes prosenus*; 6 & 7, *Alyscotermes trestus*; 8-11, *Alyscotermes kilimandjaricus*; 12, *Aganotermes oryctes*.

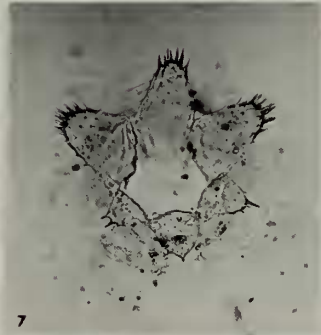
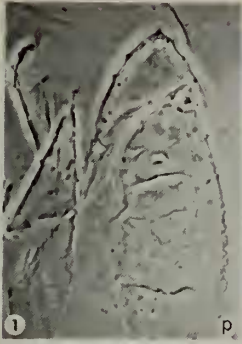


PLATE 3

Enteric valve armature. Some valves are mounted whole and viewed from side or end on, others slit and opened out. Small 'p' in lower right corner indicates use of phase contrast illumination.

FIGS 1 & 2 (latter enlarged), *Acholotermes chirotus*; 3, *Acholotermes epius*; 4, *Acholotermes imbellis*; 5 & 6, *Acholotermes tilhasus*; 7-10, *Amicotermes galenus* (10, one cushion enlarged).

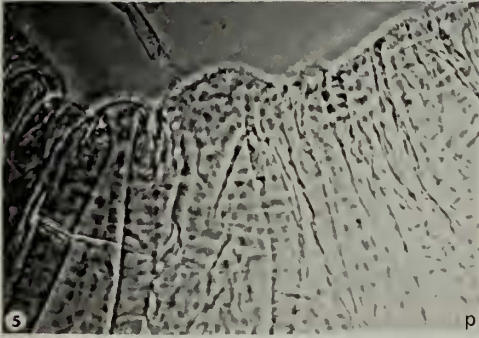
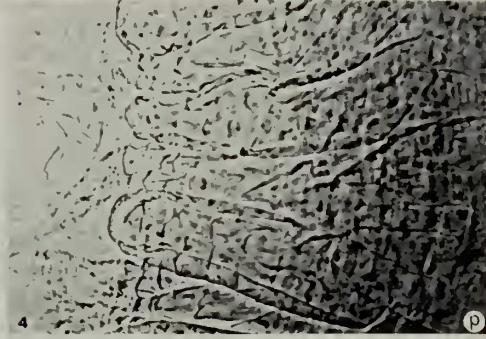


PLATE 4

Enteric valve armature. Some valves are mounted whole and viewed from side or end on, others slit and opened out.

FIGS 1 & 2, *Apagotermes stolidus*; 3 & 4, '*Ateuchotermes*' undescribed species with all cushions equally developed; 5, *Ateuchotermes tranquillus*; 6 & 7, *Ateuchotermes pectinatus*.



PLATE 5

Enteric valve armature. Valves are mounted whole and viewed from side or end on.
FIGS 1-3, *Ateuchotermes vastratus*; 4-6, *Ateuchotermes muricatus*; 7-9, *Ateuchotermes sentosus*.



PLATE 6

Enteric valve armature. Some valves are mounted whole and viewed from side or end on, others slit and opened out.

FIGS 1 & 2, *Ateuchotermes ctenoceph*; 3-5, *Ateuchotermes spinulatus*; 6-8, *Ateuchotermes retifaciens* (8, some of spines enlarged to show interlocking of hooked tips to form 'network').



PLATE 7

Enteric valve armature. Some valves are mounted whole and viewed from side or end on, others slit and opened out. Small 'p' in lower right corner indicates use of phase contrast illumination.

FIGS 1-3, *Anaoterme echinocolon*; 4 & 5, *Asagarotermes coronatus* (5, end view enlarged); 6, *Anenteotermes ateuchestes*; 7, *Anenteotermes disluctans*; 8, *Anenteotermes hemerus*.

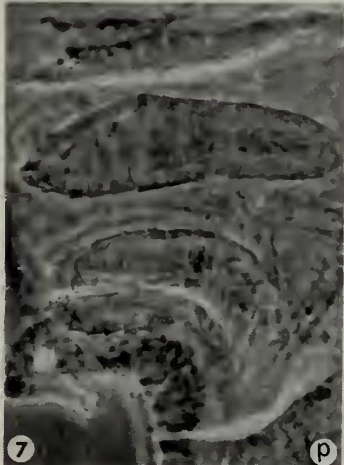
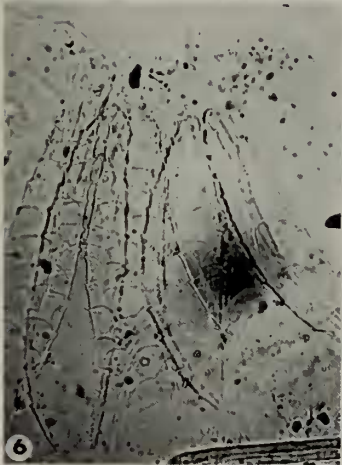
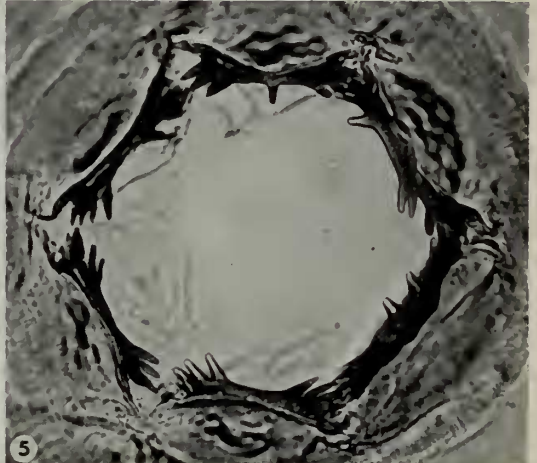


PLATE 8

Enteric valve armature. Some valves are mounted whole and viewed from side, others slit and opened out. Small 'p' in lower right corner indicates use of phase contrast illumination

FIGS 1, *Anenteotermes amachetus*; 2, *Anenteotermes nanus*; 3, *Anenteotermes cnaphorus*; 4-6, *Anenteotermes polyscolus*.

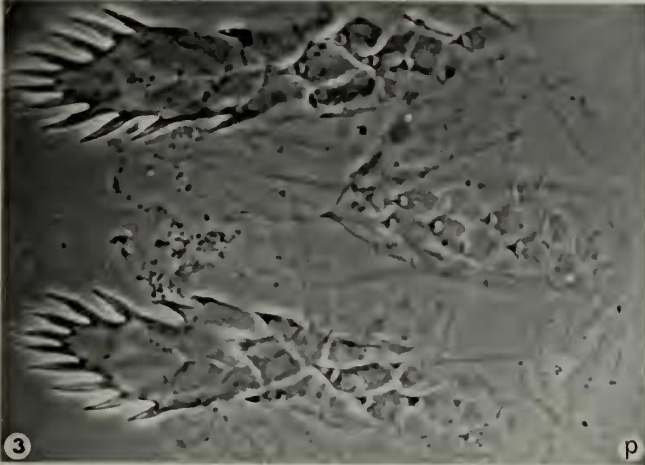
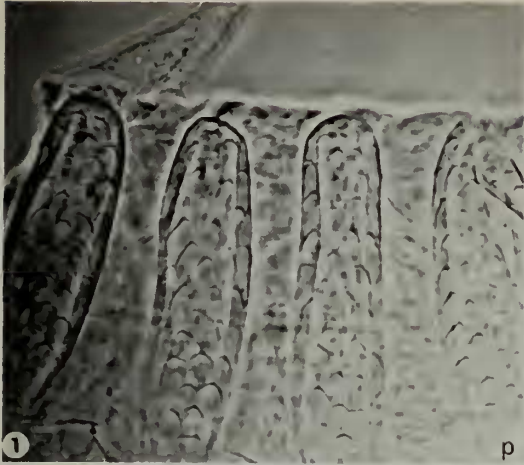


PLATE 9

Enteric valve armature. Some valves are mounted whole and viewed from side, others slit and opened out. Small 'p' in lower right corner indicates use of phase contrast illumination.

FIGS 1-4, *Adevitotermes fossor*; 5, *Adevitotermes* unnamed species from W. Africa exactly intermediate between two named spp.; 6-9, *Adevitotermes cavator* (9, single cushion and part of wall enlarged); 10, *Adaiphrotermes choanensis*; 11, *Adaiphrotermes cuniculator*; 12, *Adaiphrotermes scapheutes*.

